The Morphology and Taxonomy of *Aneilema* R. Brown (Commelinaceae)

ROBERT B. FADEN

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ABSTRACT

Faden, Robert B. The Morphology and Taxonomy of *Aneilema* R. Brown (Commelinaceae). *Smithsonian Contributions to Botany,* number 76, 166 pages, 57 figures, 17 maps, 7 plates, 1991.—Vegetative and reproductive morphology and their variation within *Aneilema,* one of the largest genera of Commelinaceae, are described in detail. The taxonomic usefulness of the various characters is considered, and floral attributes are found to be particularly important. Within the genus, great diversity is found in habit, pedicel curvature, petal color, stamen curvature, floral hair types and distribution, and seed shape and testa patterns. Anatomy, cytology, phytochemistry, and reproductive biology of *Aneilema* are treated briefly. *Aneilema* is divided into seven sections, with sections *Rendlei, Somaliensia, Brevibarbata,* and *Pedunculosa* described as new. Keys to the sections and to all 62 species recognized are provided. The 22 species comprising sections *Rendlei, Somaliensia,* and *Lamprodithyros* are treated in detail, with nine new species and five new subspecies described. One naturally occurring hybrid is also newly recognized. Two species originally described in *Aneilema* but of uncertain generic position, *A. calandrinoides* and *A. brasiliense,* are discussed in detail. A list of all specific names that have ever been included in *Aneilema* and their current status (including new combinations and new synonymy, when appropriate) is appended.

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Contents

Preface and Acknowledgments

This monograph is based on a doctoral dissertation (Faden, 1975). It differs from the thesis in several significant ways: three major portions of the original have been only briefly summarized in the present work: a chapter on cytology, which will be published as a separate paper; a section on the history and typification of *Aneilema,* which has already been published (Faden, 1978b); and a chapter on the generic relationships of *Aneilema,* which will also be published separately. As a result of new collections, three species and four subspecies, all described as new, have been added to the 1975 treatment of the three monographed sections. Two of these three species, *A. sebitense* and *A. woodii,* were treated as inadequately known taxa in the dissertation under *A. forskalii* and *A. petersii,* respectively. The third, *A. longicapsa,* and the new subspecies *A. indehiscens* subsp. *keniense* and *A. pusillum* subsp. *variabile, gypsophilum,* and *thulinii,* were not recognized in the thesis.

Among the other differences from the dissertation, the species descriptions and discussions have been shortened, and all new collections seen through 1986 have been added. For the sections that are not monographed, distributions of the species and a discussion about the naturalness of the section and taxonomic problems that remain have been added. Two of the species that were described as new in the dissertation, *A. indehiscens* and *A. tanaense,* were formally published subsequently (Faden, 1984) because the names were needed for the treatment of the family in the *Flora of Southern Africa* (Obermeyer and Faden, 1985) and other publications. Changes in the key to the species of section *Brevibarbata* and in the circumscription of *A. schlechteri* are the result of a study of that species and its relatives (Faden, 1984).

The new species of *Aneilema* described and new combinations in other genera made in the dissertation were erroneously listed in *Index Kewensis,* supplement 17 (Davies, 1987) as having been validly published in 1975, based on an on-demand copy of the dissertation that was obtained by the library of the Royal Botanic Gardens, Kew. That this listing was in error was acknowledged in the following (R.K. Brummitt, in litt., 3 March 1988):

> We are very surprised that your Commelinaceae names were taken up in I[ndex] K[ewensis]. It is certainly our policy now not to treat one-off copies produced from microfilm as effectively published, and I thought this policy had been applied for a long time. We consider that it was a mistake on our part that the names were included in Supplement 17, and we offer our apologies.... If you should re-publish any of them we would list them again from the new publication with a note about the previous entry.

The first and hitherto only valid publication of any *Aneilema* species described in Faden (1975) was in Faden (1984). The rest are published herein. The names first effectively published in *Index Kewensis* (Davies, 1987) as nomina nuda are sections *Brevibarbata* (as "Brevibarbatum"), *Pedunculosa* (as "Pedunculosum"), *Rendlei* and *Somaliensia* (as "Somaliense"), and *A. brenanianum, grandibracteolatum, lamuense, petersii* subsp. *pallidiflorum, recurvatum, succulentum,* and *usambarense.* In order to avoid further cluttering up the literature, the *Index Kewensis* citations have been omitted from the text.

With regard to combinations made in other genera in the dissertation and mistakenly listed in *Index Kewensis,* the situation is more complicated. The combinations listed for *Rhopalephora* and attributed to Faden (1975) were first validly published in Faden (1977), except for *R. monadelpha,* which was abandoned in favor of *R. micrantha* (Vahl) Faden in the latter paper and thus was never validly published. None of the combinations made in *Dictyospermum* in Faden (1975) and listed in *Index Kewensis* (Davies, 1987) has been validly published, nor will they ever be by me, for my generic concepts have changed.

ACKNOWLEDGMENTS

I am greatly indebted to the many persons who have assisted in various aspects of this research. The following are gratefully acknowledged for having supplied me with living material of *Aneilema* or related genera: Dr. P. Andrews, Dr. B.G. Briggs, Dr. G. Davidse, Mr. D.B. Fanshawe, Dr. I. Friis, Dr. A. Gentry, Mr. M.G. Gilbert, Mr. J.B. Gillett, the late Mr. J.B. Hall, Mr. K. Inoue, Mr. A.B. Katende, Mr. J. Lavranos, Dr. J.M. Lock, Mr. K.A. Lye, Dr. Gordon McPherson, Mrs. G.E. Organ, Mr. C.F. Paget-Wilkes, Mrs. J. Pawek, Dr. T. Pócs, Mr. M.G. Price, Dr. C.K. Rao, Dr. C.J. Saldanha, Mrs. J. Stewart, Mr. R.G. Strey, Dr. M. Thulin, the late Mrs. E.M. Tweedie, and Mr. J.R.I. Wood. Living materials were also supplied by the Royal Botanic Gardens, Kew, and Royal Botanic Gardens, Sydney.

I wish to thank the directors of the following institutions for the loan of specimens (abbreviations after Holmgren, Keuken, and Schofield, 1981): B, BM, BOL, BR, BRI, C, CANB, COI, EA, F, FHI, FHO, FT, G, GC, GH, K, LISC, LMA, LUA, M, NDO, NH, NSW, NU, NY, P, PAV, PRE, PUC, QRS, RO, S, SRGH, UPS, US, VEN, WAG, Z. The curators of BM, EA, K, L, MAL, MPR, PRE, and Tsavo Research Centre Herbarium allowed me to study additional specimens at their institutions.

The following are also thanked for their invaluable assistance: Dr. B.B. Chimphamba, Mr. D.B. Fanshawe, Dr. and Mrs. W.L. Handlos, Miss C.H.S. Kabuye, Dr. and Mrs. J.M. Lock, and Mr. and Mrs. A. Pooley, for extending hospitality and helping with the 1974 field work in Africa; Dr. W.H. Lewis, Dr. J. Dwyer, Dr. R. Andrews, Dr. A. Covich, and Dr. D.H. Nicolson, for reading part or all of the original thesis; the late Prof. J.P.M. Brenan, for his stimulating correspondence about *Aneilema* and other Commelinaceae and for his continuing interest in my research; Dr. Y. Suda, with whom the cytological studies were carried out jointly, for helping with all aspects of that work; the late Mr. P.R.O. Bally, Mr. P. Bamps, Mr. J.B. Gillett, Mr. J. Lavranos, and Dr. R.M. Polhill, for supplying geographic coordinates for collection localities; Dr. J. Dwyer, for assisting with some of the Latin descriptions; Dr. J. Nowicke, for preparing the scanning electron micrographs; the late Dr. J. Ridgway, for making available his Wild Dissecting Microscope; Mr. J. Lavranos, for supplying detailed ecological data for one of his *Aneilema* collections; Dr. P.H. Raven, for making all of the facilities of the Missouri Botanical Garden freely available to me; the government of Kenya, for permission to do research in that country. Reviewers Dr. W.C. Burger, Dr. D.R. Hunt, and an anonymous reviewer provided useful suggestions. Some of the line drawings were made by Mrs. Audrey J. Faden, Miss Tana Acton, Mr. Stanley Dolasinski, and Miss Alice Tangerini. Miss Susan Wiser and Mrs. Marie Uehling Kopp helped prepare the word processing copy.

The insects were determined by Dr. C.D. Michener (bees) and the Commonwealth Institute of Entomology (all but the Hymenoptera).

Financial support for field work in 1974 was provided by the National Science Foundation Doctoral Dissertation Improvement Grant No. GB-40817.

I am particularly grateful to Dr. Walter H. Lewis for guiding this research, and to Mr. J.B. Gillett and Miss C.H.S. Kabuye, Botanists-in-Charge of the East African Herbarium during the period when I was employed there as a Peace Corps Volunteer (1969–1971), for allowing me ample time for field work.

Finally, I must thank my wife Audrey J. Faden, without whose help, patience, and encouragement the original dissertation could not have been completed.

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Robert B. Faden

Introduction

The Commelinaceae are familiar to botanists of temperate North America largely through the native genera *Commelina* and *Tradescantia* and through a variety of tropical species commonly cultivated as houseplants and greenhouse ornamentals. Some Commelinaceae are used in introductory biology or botany laboratories to demonstrate cytoplasmic streaming and plasmolysis. Species with large chromosomes have been employed in research on chromosome structure and karyotype evolution. Certain *Tradescantia* clones have been used to test the mutagenicity of airborne substances (see Schairer et al., 1982); but overall, the members of this family are little utilized by man.

Aneilema is an important genus in the Commelinaceae for several reasons. It is the second or third largest genus (after *Commelina* and *Tradescantia*, depending upon the latter's circumscription), containing some 62 species. It is one of only six genera (out of 40) occurring in both the Old and New Worlds. It has been much confused taxonomically, having been circumscribed in many different ways by various authors (see Faden, 1978b,c).

The purposes of this investigation were the (1) delimitation of *Aneilema*, (2) division of the genus into sections, and (3) monographic treatment of one or more sections. The circumscription of *Aneilema* used here was arrived at through an intensive study of the morphology of all species in the genus. This was paralleled by in-depth investigations of related genera, which were then compared with *Aneilema*. The morphological studies of *Aneilema* led to its division into seven sections. Three sections comprising 22 species have been monographed.

The large size of the genus prevented an exhaustive survey of the variation in many kinds of characters. Anatomy was looked into briefly and found not to be very promising for providing specific or sectional characters, with the exception of floral hair types and distributions. Cytology, on the other hand, proved much more significant and was investigated more thoroughly. Those results will be reported in a separate publication.

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Materials and Methods

Herbarium specimens of all species have been studied (see list of herbaria from which specimens were borrowed under "Acknowledgments"). Living plants and preserved materials, including flowers, of *Aneilema* species were available as follows—the remaining species having been studied only from dried specimens:

1. Preserved material only: *plagiocapsa* (section *Amelina*); *silvaticum* (section *Brevibarbata*); *richardsiae* (section *Pedunculosa*).

2. Preserved material and living plants only from cultivation: *acuminatum, biflorum, neocaledonicum* (section *Aneilema*); *gillettii* (section *Amelina*); *longicapsa, pusillum* subsp. *gypsophilum, pusillum,* and *thulinii* (section *Somaliensia*); *forskalii, woodii, woodii* ×*forskalii* (section *Lamprodithyros*); *lanceolatum* subsp. *lanceolatum, pomeridianum* (section *Brevibarbata*).

3. Preserved material and living plants from the field and often also from cultivation: *somaliense* (section *Somaliensia*); *brenanianum, rendlei, taylorii* (section *Rendlei*); *aequinoctiale, ephemerum, hockii, johnstonii, longirrhizum, nyasense* (section *Amelina*); *calceolus, clarkei, indehiscens* (all subspecies), *lamuense, petersii* (both subspecies), *recurvatum, sebitense, succulentum, tanaense, zebrinum* (section *Lamprodithyros*); *arenicola, beniniense, brunneospermum, dispermum, dregeanum, macrorrhizum, umbrosum, welwitschii* (section *Brevibarbata*); *chrysopogon, hirtum, leiocaule, minutiflorum, nicholsonii, pedunculosum, spekei, termitarium* (section *Pedunculosa*).

The taxa for which living material was obtained only after the completion of Faden (1975) are *forskalii, indehiscens* subsp. *keniense, lanceolatum* subsp. *lanceolatum, longicapsa, pomeridianum, pusillum* subsp. *gypsophilum,* subsp. *pusillum* and subsp. *thulinii, sebitense, woodii, woodii* ×*forskalii.*

To determine pollen viability, pollen grains from anthers of

mature buds, preserved in three parts absolute ethanol and one part glacial acetic acid, were stained with cotton blue. Pollen grains for scanning electron microscopic study were acetolyzed according to the procedure of Erdtman (1966), vacuum coated with gold, and examined and photographed with a Cambridge Stereoscan Mark IIa Scanning Electron Microscope. Capsule walls and seeds for SEM study were coated and examined as above. Seeds for light microscopic study were photographed with a Wild Dissecting Microscope.

Stem and leaf transverse sections were made freehand from living and preserved material and stained with 0.01% methylene blue for 30 to 60 minutes. They were then irrigated with 10% glycerine and stored as semi-permanent mounts. The *Aneilema* species investigated were as follows: *acuminatum, neocaledonicum* (section *Aneilema*); *taylorii* (section *Rendlei*); *somaliense* (section *Somaliensia*); *aequinoctiale* (section *Amelina*); *petersii* subsp. *pallidiflorum, succulentum, zebrinum* (section *Lamprodithyros*); *spekei* (section *Pedunculosa*).

Paired petal color was determined by means of an R.H.S. Colour Chart (1966). Comparisons with the color patches of the chart were made in daylight in bright shade, almost always by two observers. All paired petal colors noted in the population were recorded.

Floral hairs were studied from preserved mature buds or, occasionally, preserved or fresh flowers. The buds or flowers were dissected into separate organs, which were mounted whole or slightly macerated, when necessary. These were stained with 0.01% methylene blue and irrigated with 10% glycerine as above. Glandular cells stained darkly in less than 60 seconds. Other cells stained weakly or not at all, even after 60 minutes. The species examined are listed in Tables 3, 4, and 5.

Buds for meiotic chromosome counts were collected in the field or from cultivated plants. Root tips for mitotic counts were collected from greenhouse grown plants. The procedures followed were those of Faden and Suda (1980).

Species descriptions were drawn up using a variety of materials, including herbarium specimens, and (when available) living plants, preserved flowers and inflorescences, separately collected capsules and seeds, detailed descriptions of morphology made from living plants, and color transparencies. Of the 22 species studied in detail, 14 were seen in the field and were later cultivated, another four were cultivated from material obtained from other collectors, and only four (*A. usambarense, A. grandibracteolatum, A. obbiadense, A. benadirense*) had to be studied exclusively from herbarium specimens. Among the 40 species belonging to sections that are not monographed, 28 were observed in the field or under cultivation, and the rest had to be studied from only dried or preserved specimens.

One hundred and twenty-one populations representing 32 *Aneilema* species plus four infraspecific taxa were observed in the field in Africa (Ghana, Kenya, South Africa, Zambia, Malawi, and Tanzania) from January to August 1974. Specimens were collected and ecological notes made for every population. When possible, detailed notes were made of vegetative and reproductive morphology, including paired petal color, on specially designed data sheets. Further notes were made on the reproductive condition of the plants, e.g., whether mature capsules were present, flowering times, and the presence of pollinators, which were collected whenever possible. Color transparencies were taken of the flowers and sometimes of the inflorescence and habit using a Miranda DR single-lens reflex camera, Kodachrome II 35 mm film, a Honeywell Strobonar 100 electronic flash and extension tubes for close-ups. In addition to dried specimens, materials frequently collected included flowers and vegetative organs preserved in FAA, separate capsules and seeds placed in seed packets, buds fixed for cytological study, and cuttings or whole plants for later cultivation.

Plants were cultivated at the Missouri Botanical Garden until 1976, at the University of Chicago 1976–1980, and at the Smithsonian Institution Department of Botany greenhouse from 1980 until the present.

Most plants studied in cultivation were derived from the 1974 field collections. Other materials for cultivation came from earlier field collections made by the writer, from the writer's 1977 Kenyan collections, from plants or seeds collected by various persons at the writer's request (see "Acknowledgments"), and from materials in cultivation at botanical gardens. These plants were described and photographed as above. Flowers and other materials were collected from the cultivated plants for later study. Preserved flowers of some species were studied at the Royal Botanic Gardens, Kew, or obtained on loan from that institution.

Determinations of habit types have been based largely on field notes and living plants. Descriptions of vegetative and inflorescence morphology have utilized dry specimens for the most part, being supplemented by data from living plants, when available. In contrast, whenever possible, floral descriptions have been derived almost entirely from living and preserved materials, with data added from field notes and color transparencies. When such material was lacking, pressed flowers (or their remains) and buds, soaked in a solution of Aerosol OT and usually dissected in situ, provided the basis for the descriptions. In order to avoid ambiguity, the manner of measuring certain vegetative and floral parts has been described under the relevant structures.

All specimens seen through 1986 of the species in sections *Rendlei, Somaliensia,* and *Lamprodithyros* have been cited under the species (also see Appendix III). The countries are listed from west to east and north to south. For political subdivisions, listed alphabetically within the countries, the *Flora of Tropical East Africa* (1952–) has been used for Uganda, Kenya, and Tanzania, *Flora Zambesiaca* (1960–) for Mozambique, and the *Times Atlas of the World* (1971) for other countries. For a few countries, political subdivisions were unclear and have been omitted. The system proposed by

Edwards and Leistner (1971) has been used for citing South African collections. Only specimens seen have been mapped. All lectotypes are those of the writer unless otherwise stated.

Morphology of *Aneilema*

I may here mention, for the encouragement of parties who may have an opportunity of collecting specimens, that I have learned in the course of their investigation, that much more can be done with dried specimens than I previously supposed possible, and would therefore urge their collection, as I feel quite convinced that the Commelynaceae is much richer in species than the latest publications would lead one to suppose. (Wight, 1853:28.)

Introduction to Morphology

The Commelinaceae is one of the most awkward families to study using dried specimens because the deliquescent flowers are normally poorly, if at all, preserved. The difficulty in making use of such material is no doubt a contributing factor to the paucity of modern monographic studies in the family. In the present investigation, living material has been utilized whenever possible. However, the large number of taxa surveyed has necessitated an examination of numerous herbarium specimens. For a number of species this has been the only kind of material available. Like Wight (1853), I have been pleasantly surprised as to how much could be learned from dried specimens, particularly from those with mature flower buds.

The genera of Commelinaceae are defined largely on the basis of morphological characters. The total morphological variation in *Aneilema* has never been studied. The most useful contributions have been those of Brückner (1926, 1930), Brenan (1952), and Morton (1966). These studies have either been limited to a few characters (Brückner, 1926, 1930; Brenan, 1952) or have been geographically biased and the generalizations made not always applicable to the genus as a whole (Morton, 1966).

In the present account, an attempt has been made to examine the morphology of all species in the genus. The extent to which each species has been studied depended upon the type of material available and whether the species belonged to one of the sections selected for detailed taxonomic investigation. All aspects of morphology have been examined, but greatest emphasis has been placed on floral and seed morphology.

Vegetative Morphology

Habit.—*Aneilema* shows great diversity in habit. I recognize 17 habit types (Figures 1–3), but the boundaries between adjacent types are not always clean-cut. The basic type (IA) is a decumbent perennial in which the main shoot is overtaken by lateral shoots that in turn are overtaken by other lateral shoots. The decumbent perennial has given rise to a variety of other habit types: less decumbent to ascending or erect perennial or annual (IB and IC); mat-forming perennial or annual (IIA1 and IIB); rhizomatous perennial with fibrous roots (IIA2); long-trailing, sometimes looping or scrambling perennial (IIA3); ascending perennial that produces occasional long-trailing shoots that give rise to new plants (IIA4). The erect to ascending perennials and annuals (IC) have themselves produced two major lines of habit types. One is a series of reduced annuals (IIIA, IIIB, and IIIC) that secondarily may become decumbent again (IIIB). The other line consists of tuberous-rooted perennials. Among these the basic type (IVA) has sessile root tubers, a single or sometimes two subterranean growing points that persist only one or two growing seasons, and a moderately well-branched, ascending shoot system. From this type have arisen forms with stalked, distal tubers (IVB1), more persistent shoot bases that become shortly rhizomatous (IVB2), or reduced shoot systems (IVB3). In the type with stalked tubers, the shoots may sometimes root at the lower nodes (IVC1). The stalked tuber type has also given rise to forms with dimorphic vegetative and reproductive shoots (IVC2). The reproductive shoots are sometimes produced before the vegetative shoots during the growing season.

Varying amounts of dieback occur in the perennial species at the end of the growing season. In the decumbent to erect, fibrous-rooted species, the lower portions of the shoots normally survive and produce new growth from axillary buds during the next growing season. In species with subterranean storage organs, the entire aerial shoot system or the greater part of it (depending upon the species) dies during the dry season. The shoots may gradually die back like the fibrous-rooted perennials or they may abscise at the base.

It is sometimes difficult to determine whether a plant is an annual or a perennial. As used here, annuals are monocarpic plants that, under natural conditions, live less than a year. Perennials live more than one year and have the potential to flower and fruit more than once. Two examples will serve to illustrate the problem in applying these definitions.

Aneilema petersii subsp. *pallidiflorum*, new subspecies, may be distinctly annual. However, when the plants produce shortly decumbent shoots, which they often do, they may appear perennial, even in the field. From prolonged observations of populations in the Tsavo area of Kenya, it was learned that even these perennial-appearing plants are monocarpic and die after fruiting. Fitting these plants, however, into the above definition of an annual is complicated by the fact that they normally require two growing seasons, at least in this area, to complete their life cycle. The seeds germinate during the short rains (November to December) but, typically, the plants do not flower then. Despite the absence of clearly adapted water storage organs, many plants survive a three-month dry season, flower and fruit during the long rains (April to May), and then die. Since the entire life cycle does occur within 12 months (although over two calendar years), and there is only one flowering period, the plants are considered annuals.

Plants of *Aneilema sebitense*, new species (*Gilbert & Thulin 266*) and *A. forskalii* (*Gilbert & Thulin 969*), when grown from seed, developed identically, rapidly producing numerous

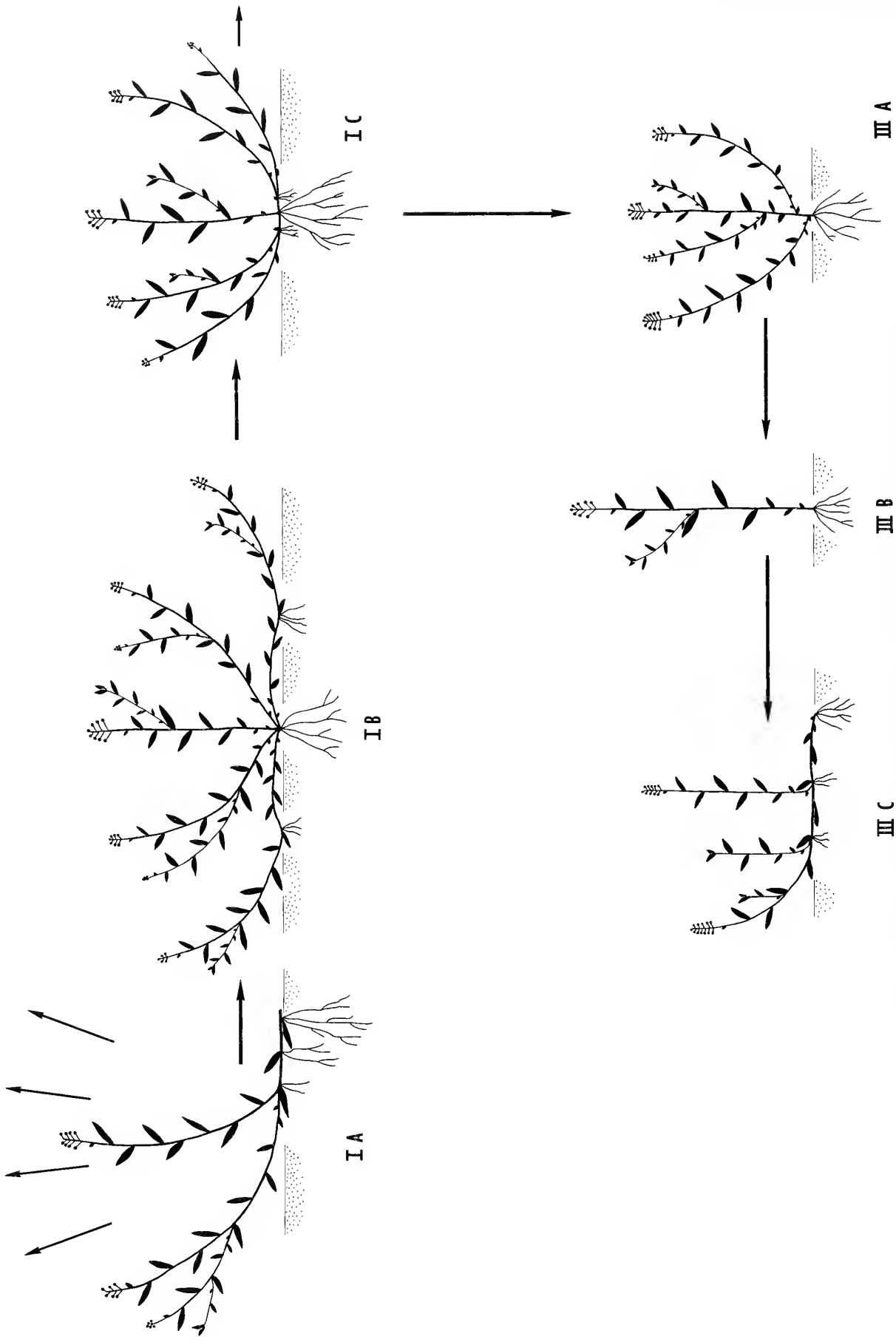


FIGURE 1.—*Aneilema* habit types. Fibrous-rooted perennials and annuals: IA, decumbent; IB, ascending, the longer shoots somewhat decumbent basally; IC, ascending; IIIA, ascending to erect; IIIB, erect; IIIC, procumbent.

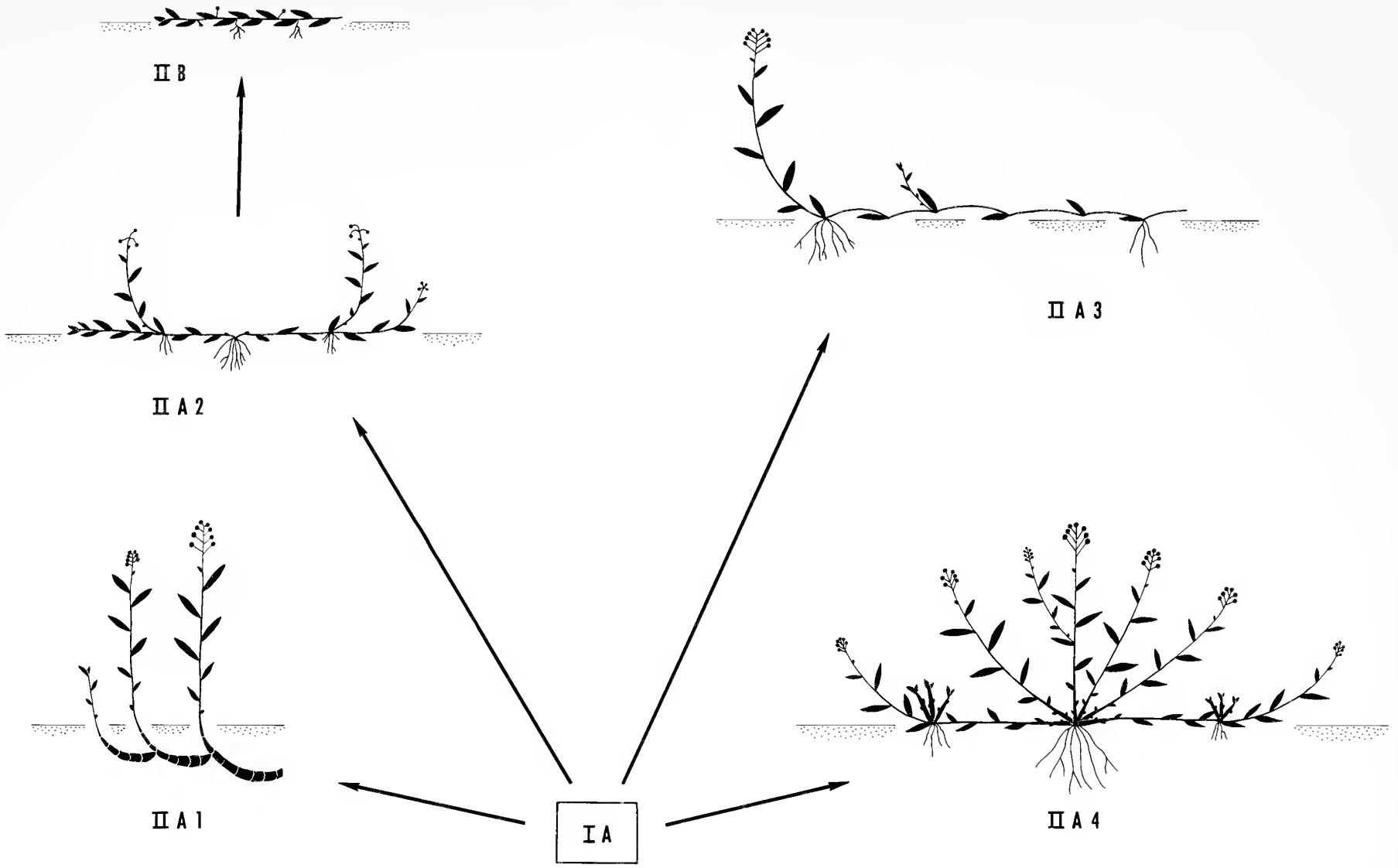


FIGURE 2.—*Aneilema* habit types. Fibrous-rooted perennials and annuals: IIA1, rhizomatous; IIA2, mat-forming with ascending flowering shoots; IIA3, trailing or looping; IIA4, ascending, the longer, decumbent shoots producing plantlets (otherwise like IB); IIB, repent.

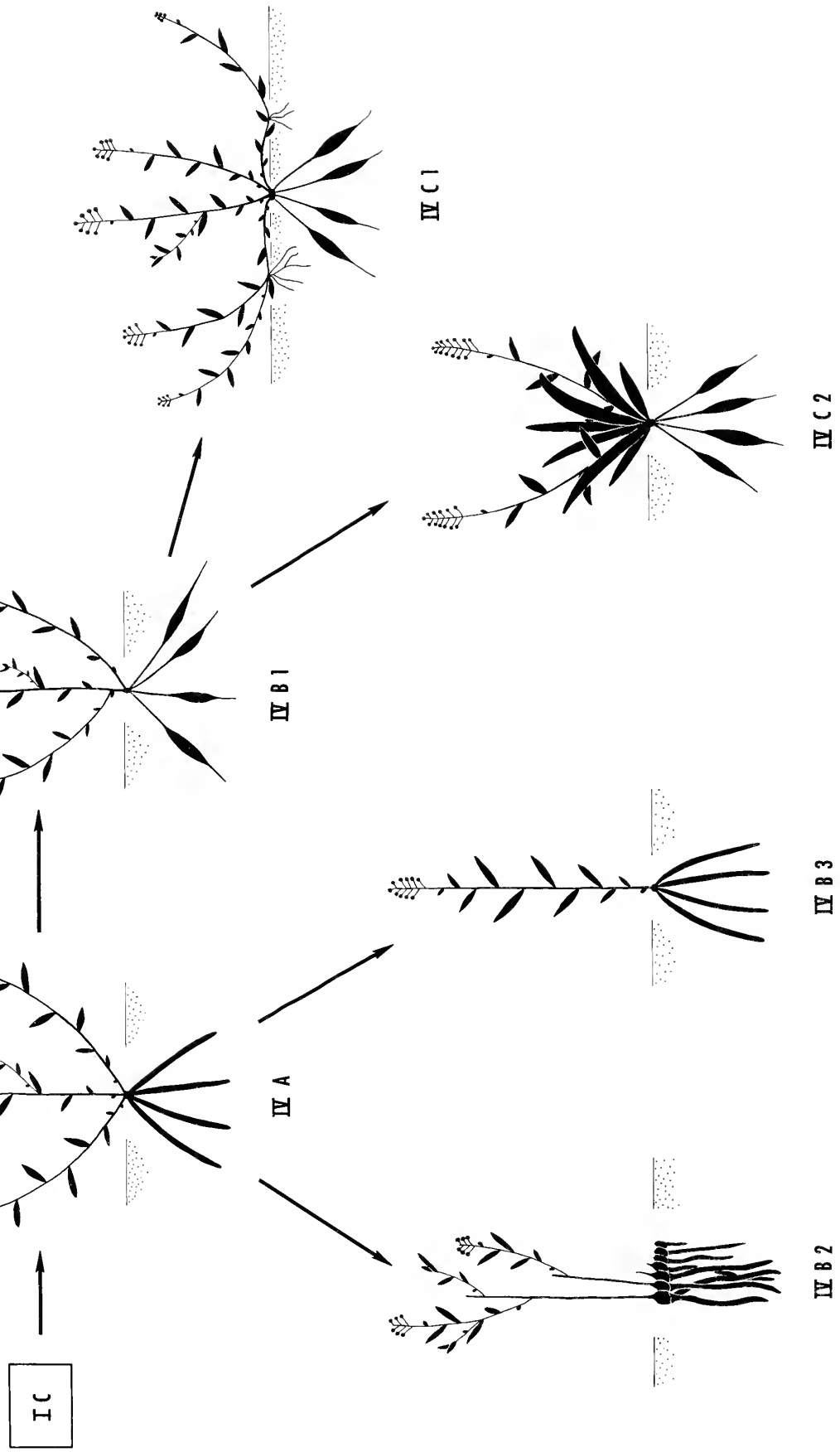


FIGURE 3.—*Aneilema* habit types. Tuberous-rooted perennials: IVA, ascending to erect, with sessile tubers; IVB1, like IVA but with stalked tubers; IVB2, rhizomatous; IVB3, erect, with sessile tubers; IVC1, like IVB1, but longer shoots decumbent basally; IVC2, erect to ascending with dimorphic shoots, the vegetative forming rosettes.

shoots with terminal and axillary inflorescences, a characteristic of annuals; but whereas the plants of *A. forskalii*, proved to be annual by continuing this pattern of growth and eventually losing vigor and dying, those of *A. sebitense* began to produce strong vegetative shoots and have been cultivated continuously since 1976. From this evidence and later cultivation of plants from two additional populations of *A. forskalii* (*Wood 1997* and *2895*) and one of *A. sebitense* (*Faden & Faden 77/803* and *77/803A*), it was concluded that *A. forskalii* is always annual. On the other hand, although *A. sebitense* is perennial, young plants appear capable of functioning as annuals during very short rainy seasons. Plants of this species may thus be considered perennials or facultative annuals. The perennial habit of this species would be entirely unpredictable, based solely on the morphology of the young plants.

Perennials and annuals are known to occur within five species of *Aneilema*. In *A. petersii* and *A. paludosum*, the perennials are considered sufficiently differentiated to be treated as separate subspecies. In *A. taylorii*, *A. tanaense*, and *A. calceolus*, they are not distinct enough to merit taxonomic recognition. In *A. taylorii* the perennials occur at higher elevations and probably in moister situations than the annuals. In the other two species the perennials occur as peripheral populations in otherwise annual species.

Most other species show relatively little variation in habit when only mature plants are considered. In the course of development they may exhibit other habit types transitionally. For example, many decumbent perennials are erect to ascending in their early stages. Other variation, such as the degree of branching exhibited by annuals, may be caused by edaphic factors or the length of a particular growing season.

An exception is *A. hockii* in which fibrous-rooted decumbent, fibrous-rooted rhizomatous, and tuberous-rooted, ascending perennials occur. A great deal of variation in the amount of branching is also present within some of these types. Further study is required to determine how to treat these forms of *A. hockii* taxonomically.

For convenience, the 17 habit types recognized can be reduced to three general categories: perennials lacking specialized, subterranean storage organs, perennials with such organs, and annuals. The *Aneilema* species with each type are as follows:

Perennials lacking specialized, subterranean storage organs: *acuminatum*, *biflorum*, *neocaledonicum* (section *Aneilema*); *aequinoctiale*, *hockii*, *nyasense* (section *Amelina*); *rendlei*, *taylorii*, *usambarense* (section *Rendlei*); *calceolus*, *clarkei*, *indehiscens*, *petersii* subsp. *petersii*, *recurvatum*, new species, *sebitense*, *succulentum*, new species, *tanaense*, *woodii*, new species, *zebrinum* (section *Lamprodithyros*); *beniniense*, *dispermum*, *dregeanum*, *silvaticum*, *umbrosum* (section *Brevibarbata*); *leiocaule* (section *Pedunculosa*).

Perennials with specialized, subterranean storage organs: *sclerocarpum*, *siliculosum* (section *Aneilema*); *gillettii*, *hockii*, *johnstonii*, *longirrhizum*, *plagiocapsa* (section *Amelina*); *brenanianum*, new species (section *Rendlei*); *longicapsa*, new species, *obbiadense*, *pusillum*, *somaliense* (section *Somaliensia*, new section); *homblei*, *lanceolatum*, *macrorrhizum*, *paludosum* subsp. *pseudolanceolatum*, *pomeridianum*, *setiferum*, *welwitschii* (section *Brevibarbata*, new section).

Annuals: *aparine?* (section *Aneilema*); *ephemerum* (section *Amelina*); *calceolus*, *forskalii*, *lamuense*, new species, *petersii* subsp. *pallidiflorum*, *tanaense* (section *Lamprodithyros*); *angolense*, *arenicola*, *brunneospermum*, *mortonii*, *paludosum* subsp. *paludosum* and subsp. *pauciflorum*, *schlechteri* (section *Brevibarbata*); *chrysopogon*, *hirtum*, *minutiflorum*, *nicholsonii*, *pedunculosum*, *richardsiae*, *spekei*, *termitarium* (section *Pedunculosa*).

Species of unknown habit: *grandibracteolatum*, new species (section *Somaliensia*); *benadirense* (section *Lamprodithyros*).

ROOTS.—Roots in mature plants are all adventitious. Seedlings of *A. umbrosum* have been observed to develop such roots when only 24 hours old. These adventitious roots rapidly overtake the radicle. In older plants adventitious roots are produced from nodes—often several from a node—that are close to or in contact with the substrate. In some species they are produced only from subterranean shoots.

Roots may be fibrous or variously thickened. The latter are collectively termed tuberous in this account. Tuberous roots may be of uniform thickness for their entire length, e.g., *A. longirrhizum*, but, more commonly, they taper from their bases or at both ends. The fusiform tubers are sessile in some species, e.g., *A. pusillum*, and shortly to longly stipitate in others, e.g., *A. lanceolatum*. Stipitate, tuberous roots have been found to reach a length of 60 cm (including the stipe) in *A. somaliense*.

Aneilema hockii and *A. paludosum* are the only species in the genus that include both fibrous-rooted and tuberous-rooted plants. In *A. hockii* the type of root system has been found to be under genetic control and is maintained in cultivation. Cuttings from each type produce the same kind of roots as the plant from which they were taken. Tuberous root systems have also been reproduced by shoot cuttings of *A. brenanianum*, *A. gillettii*, and *A. welwitschii*, all tuberous-rooted species.

Aerial roots have been observed on a cultivated plant of *A. somaliense*. Short lateral shoots produced such roots from their bases. The thus formed plantlets were easily detachable from the main shoots and could function as independent plants. This peculiar vivipary has not been observed in herbarium specimens of *A. somaliense* nor in any other *Aneilema* species. It must therefore be considered an artifact of cultivation.

SHOOTS.—In mature plants of most *Aneilema* species there is neither a distinct main shoot nor a single, clear, sympodial axis, but rather a diffuse branching, which is here termed a diffuse shoot system. Such branching systems were considered sympodial by Brückner (1926), who used the term for any shoot system that was not distinctly monopodial. *Aneilema beniniense* and *A. aequinoctiale* are examples of species with diffuse shoot systems.

Sympodial shoots do occur in *Aneilema*, but they are

uncommon. They are largely confined to rhizomatous species such as *A. brenanianum* and *A. obbiadense,* in which the rhizomes are sympodial, being composed of the bases of successive lateral shoots. This type of branching never results in leaf-opposed inflorescences, as in *Commelina* and a few other genera of Commelinaceae with sympodial shoots, because the sympodial growth occurs at the base of the flowering shoot, rather than at the apex. Distinctly monopodial shoots systems are also infrequent in *Aneilema.* They occur only in annuals and tuberous-rooted perennials with reduced shoot systems. Even in these species, the main shoot tends to flower and die before the lateral shoots and is, in that sense, overtaken by them. Monopodial shoot systems are often the result of poor growth conditions: plants of the same species growing in more favorable situations may produce diffuse branching systems. Taxa in which monopodial shoot systems have been noted include *A. hockii, A. petersii* subsp. *pallidiflorum, A. nicholsonii,* and *A. termitarium.*

The shoots of *Aneilema* species vary from monomorphic to strongly dimorphic. In the monomorphic types there is no differentiation into vegetative and reproductive shoots. In other species, e.g., *A. neocaledonicum* and *A. calceolus,* the flowering shoots differ from the vegetative shoots only in being erect or ascending while the latter are repent. In *A. clarkei,* which has a similar habit to the above named species, the leaves on the vegetative shoots are uniform in size and shape; those on the flowering shoots are very diverse (see p. 133).

Strongly dimorphic shoots are produced in only a few species. The flowering shoots in *A. lanceolatum* subsp. *subnudum* have very reduced leaves, while the vegetative shoots, which are often produced later in the season (Morton, 1966), have distinctly longer leaves. In *A. pomeridianum* the flowering shoots are elongate and have relatively small leaves; the vegetative shoots form basal rosettes of longer leaves (see habit type IVC2, Figure 3).

Lateral shoots arise from axillary buds within sheaths. Such shoots may emerge from the tops of the sheaths or they may perforate them. Emergent or non-perforating shoots sometimes cause the sheaths to split more or less irregularly along the fused edge. Perforating shoots are more common than non-perforating ones and characterize species of sections *Aneilema* and *Lamprodithyros.* Non-perforating shoots are typical of sections *Brevibarbata* and *Pedunculosa.* Within plants of many species normally having one shoot type, a few shoots of the other type may be present.

A lateral shoot always has a bladeless sheath or prophyll at its base. In some *Aneilema* species an axillary bud within the prophyll may give rise to another shoot that in turn has a prophyll at its base. Successive shoots may arise in this fashion and produce a cluster of up to seven shoots at a node. Shoots arising from prophyllar buds have been noted in 11 *Aneilema* species (*arenicola, brunneospermum, calceolus, hirtum, indehiscens, minutiflorum, pedunculosum, spekei, tanaense, termitarium, zebrinum*), nine of which are annuals. It is likely to be found in most annual species of the genus. Such branching has previously been reported in the Commelinaceae only in *Tinantia* (Tomlinson, 1969).

Leaves are produced on the lateral shoots above the basal prophyll in a distinctive sequence of shapes and sizes. The first leaf always has a very small and broad lamina. Successive leaves show a gradual increase in total length and width and in the ratio of length to width. In most species a petiole is also developed by about the third or fourth leaf above the prophyll. Successive leaves have longer petioles.

Towards the inflorescence there is another sequence of leaf shapes and sizes. This transition may be abrupt or gradual and always includes some reduction in leaf length and elimination of the petiole (when present in the lower leaves). The uppermost leaf below the inflorescence is sometimes highly modified and is termed the inflorescence bract in this account. It is discussed in more detail under the inflorescence.

The middle internodes of the lateral shoots are generally the longest. The upper are often very strongly reduced. A sequence of leaves and internode lengths on a lateral shoot of *Aneilema umbrosum* subsp. *ovato-oblongum* is shown in Figure 4.

In most *Aneilema* species there is a region of the lateral shoots, between the basal and apical transition zones, in which leaf size and shape and internode length are relatively uniform. This region may be short or long, according to the species.

The sequence of leaf shapes and sizes and internode lengths in the lateral shoots is very similar to the sequence that occurs in the main shoot. The prophyll of the lateral shoot is analogous (or homologous?) to the cotyledonary sheath at the base of the main shoot in the seedling.

Leaves in *Aneilema* are always alternate and are either spirally or distichously arranged on the shoots. The spiral arrangement is much more common and is the sole type present in sections *Aneilema, Rendlei, Brevibarbata,* and *Pedunculosa.* In some species of section *Aneilema,* e.g., *A. neocaledonicum,* the leaves of the repent vegetative shoots are sometimes two-ranked, but they are clearly spirally attached to the stems.

Both distichous and spiral arrangements occur in sections *Amelina, Somaliensia,* and *Lamprodithyros.* The species in which distichous leaves have been noted are *A. aequinoctiale, A. hockii, A. longirrhizum,* and *A. nyasense* (section *Amelina*); *A. pusillum* (section *Somaliensia*); and *A. calceolus, A. clarkei, A. lamuense, A. petersii, A. succulentum, A. tanaense,* and *A. zebrinum* (section *Lamprodithyros*).

The constancy within a species of the distichous arrangement is variable. In *A. aequinoctiale, A. nyasense, A. calceolus, A. clarkei, A. lamuense, A. succulentum,* and *A. zebrinum,* all lateral shoots always have distichously arranged leaves. This is also the case for most shoots of *A. tanaense.* In some shoots of this species, however, the arrangement changes to spiral towards the inflorescences. Plants of *A. petersii* with distichous leaves on the lateral shoots have been noted in only two populations; it is unknown whether all plants of these populations have this leaf arrangement. In *A. hockii* relatively

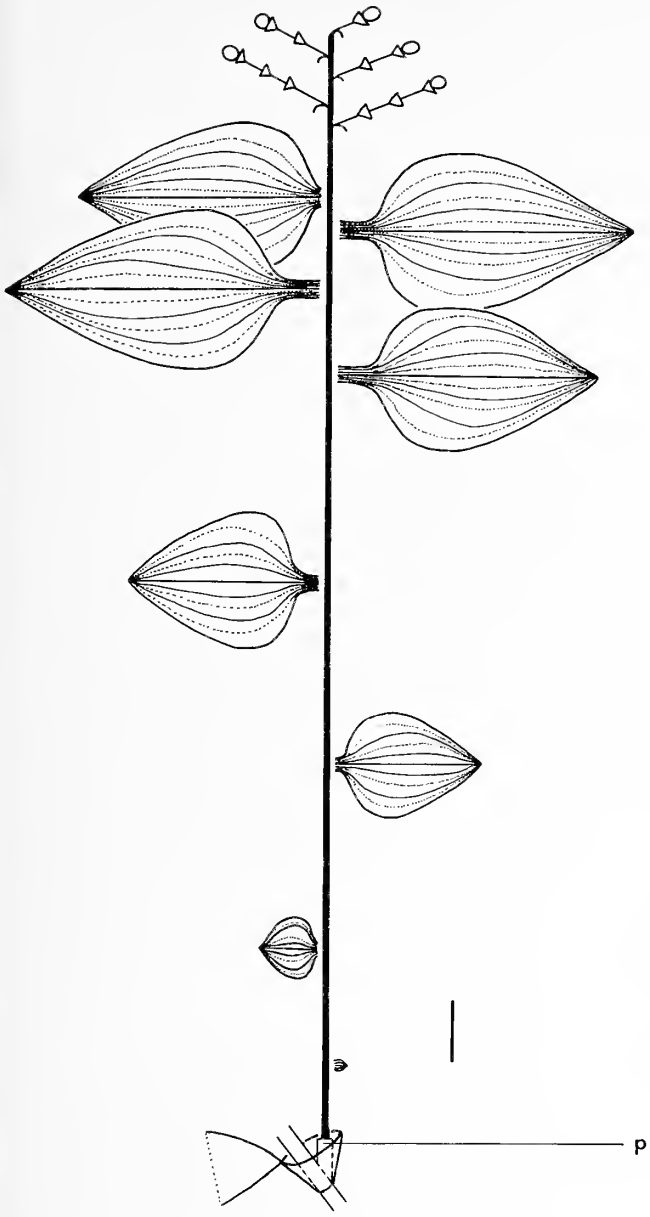


FIGURE 4.—Sequence of leaf shape and size and internode length in a lateral shoot of *Aneilema umbrosum* (Vahl) Kunth subsp. *ovato-oblongum* (P. de Beauvois) J.K Morton (p = prophyll). From *Lye & Katende 6235* in cultivation. (Bar = 1 cm.)

few populations have distichous leaves, and none has exclusively this arrangement. In plants of these populations many individual shoots have a mixture of spiral and distichous arrangements. The last situation also obtains to the single population of *A. longirrhizum* seen in the field.

The distichous leaf arrangement is commonly associated with the mat-forming habit in such species as *A. succulentum* and *A. zebrinum*. However, *A. aequinoctiale* and the populations of *A. hockii* with this leaf arrangement have erect to decumbent shoots that do not form mats. Furthermore, other mat-forming species, e.g., *A. neocaledonicum* and *A. biflorum*, have spirally arranged leaves. Seedlings of seven of the 10 species that typically or occasionally have a distichous leaf arrangement on the lateral shoots have been observed to have, as the normal condition, a spiral leaf arrangement on the primary shoot. In *A. lamuense*, *A. petersii*, and *A. tanaense*, the spiral arrangement is maintained right up to the inflorescence. In *A. calceolus* the mainshoot could not be identified with certainty in the mature plant. This probably is indicative that the leaf arrangement of the main shoot changes to distichous when the shoot becomes repent. The seedlings of *A. aequinoctiale*, *A. succulentum*, and *A. zebrinum* have not been followed to maturity.

The presence of only spiral leaf arrangements in the primary shoot of all 23 *Aneilema* species in which seedlings have been observed (*acuminatum, aequinoctiale, arenicola, beniniense, brunneospermum, calceolus, ephemerum, hirtum, indehiscens, johnstonii, lamuense, minutiflorum, pedunculosum, petersii, rendlei, spekei, succulentum, tanaense, taylorii, termitarium, umbrosum, welwitschii, zebrinum*), and the subsequent development of a distichous arrangement in the lateral shoots of some of these species support the hypothesis that in the Commelinaceae the spiral arrangement (radial symmetry) is the primitive condition and the distichous arrangement (dorsiventral symmetry) the derived one (Clark, 1904). The data for *Aneilema* do not support the hypothesis of Tomlinson (1966) that the distichous arrangement is the juvenile state and the spiral arrangement the adult condition.

INTERNODES.—Internodes are generally terete, succulent, and green. In *A. succulentum* they are sometimes laterally compressed. In all species of dry habitats, the internodes of persistent aerial shoots become shriveled during the dry season. The fleshiness of the internodes also varies according to the species. The Australo-Oceanic species have less succulent internodes than the African species. Internodes in some *Aneilema* taxa may be striped or suffused with purple, the color sometimes becoming more pronounced during the dry season.

LEAVES.—*Aneilema* leaves are typical of the family and are always simple with unlobed, entire-margined, parallel-veined laminae. The sheaths are closed except occasionally in the uppermost leaves of the flowering shoot where they may be only slightly fused basally or even completely free. The formation of a lateral shoot sometimes causes the sheath to split. Commonly the sheaths persist after the laminae have died. In a few species, e.g., *A. brenanianum*, the sheaths are very long and completely cover the lower portions of the flowering shoots, protecting them from desiccation during the dry season. In most species the sheaths are ciliate at the apex.

Laminae are generally herbaceous and pubescent on both surfaces and on the margins. In a few species the laminae are somewhat succulent, but except in *A. pusillum*, they are not as fleshy as certain species of other genera of Commelinaceae, such as *Cyanotis*, *Murdannia*, and *Tradescantia*. The laminae in *Aneilema* have symmetric bases (except *A. succulentum*),

which in many species are narrowed into petioles. Although these are not true petioles in the sense used for dicotyledons, the term "petiolate" is employed here to conform with common usage. Generally the laminae are entirely green, but in some species they may become suffused or mottled with purple or maroon, particularly in the dry season. In many species the laminae are discolorous, the abaxial surface being paler or sometimes gray-green. Stomata are present predominantly or exclusively on the abaxial surface.

The great variation in lamina shape and size present in every individual plant of *Aneilema* as a result of the developmental sequences in the shoots would tend to obscure specific characters and interspecific differences if the full range of variation were included in the species descriptions. Therefore, descriptions of the leaves are based entirely on the larger laminae present on the shoots. Lamina length always includes the petiole, when present.

Mature leaves in all but two *Aneilema* species that have been seen alive have involute vernation. The exceptions are *A. pomeridianum*, which consistently had convolute (including supervolute) vernation, and *A. pusillum*, the very succulent leaves of which were slightly conduplicate to nearly flat.

In many species, the first leaf of the seedling has a convolute vernation. This has been observed in single populations of *A. calceolus* (four seedlings), *A. ephemerum* (four), *A. johnstonii* (seven), *A. lamuense* (one), *A. pedunculosum* (eight), *A. spekei* (two), *A. tanaense* (34), and *A. termitarium* (four), and in two populations of *A. hirtum* (total of four seedlings). Solely involute vernation in the first seedling leaf has been recorded in single populations of *A. acuminatum*, *A. aequinoctiale*, *A. beniniense* (~10 seedlings), *A. petersii* subsp. *pallidiflorum* (four), *A. umbrosum* subsp. *ovato-oblongum*, and *A. welwitschii* (two). Both types of vernation have been found in two populations of *A. welwitschii* (one seedling with each type in both populations) and in one of *A. minutiflorum* (three seedlings with involute vernation, one with convolute).

In all of the above species, except *A. welwitschii*, the second and every subsequent leaf of the seedling have the involute vernation of mature plants. In a few seedlings of *A. welwitschii* the second seedling leaves had a convolute vernation, but successive leaves all had the adult type.

The significance of the above observations is unclear. The two types of vernation present in the seedlings do not separate species along sectional lines. Involute vernation is clearly the usual type in mature plants of nearly all *Aneilema* species, so the convolute vernation observed in the first leaves of some seedlings may be considered a developmental stage. Perhaps it results from the very narrow lamina in the seedlings. The only species in which convolute vernation has been noted in mature plants, *A. pomeridianum*, also has a very narrow lamina, but so does *A. brenanianum*, which consistently has involute vernation.

Reproductive Morphology

Inflorescences.—The basic type of inflorescence in *Aneilema* is a terminal thyrse consisting of several to many cincinni attached to a central axis, the inflorescence axis (Figure 5; Plates 1*g*, 2*c–e,m,o*, 4*i,m,o*). The designation of this raceme of cincinni, the *Wickeltraube* of Eichler (1875), as a thyrse follows the usage of Clarke (1881a), Pichon (1946), Brenan (1966), and Faden (1974). Most authors, however, have termed such inflorescences panicles (Bentham, 1849; Bentham and Mueller, 1878; Bentham and Hooker, 1883; Schumann, 1895; Clarke, 1897, 1901; Hutchinson, 1934, 1959; Morton, 1966). The differences are not due to varying interpretations of the inflorescence morphology but rather to diverse uses of "panicle" and "thyrse." The definition of a thyrse (or thyrsus) as a "panicle-like cluster with main axis indeterminate and the lateral axes determinate" (Lawrence, 1951) has been followed here. *Aneilema* inflorescences conform to this definition in that the cincinni flower in an acropetal sequence; therefore the inflorescence axis is indeterminate. The cincinni themselves are determinate, because every flower is morphologically terminal.

Aneilema thyrses show great variation in size, density, number and arrangement of the cincinni, and in position on the plant. Thyrses are commonly 2–15 cm long, but they can reach a length of at least 25 cm in *A. aparine* and *A. gillettii*. The number of cincinni per inflorescence has a characteristic range for each species and can be as many as 55 (or perhaps more in some forms of *A. beniniense*). In a few species, e.g., *A. clarkei*, every thyrse is composed of a single cincinnus (Plates 3*p*, 4*e,g*).

The density of the inflorescence is a function of the length of the inflorescence axis, the number of cincinni attached to it, and the length of the cincinni. The terms lax, moderately lax, moderately dense, and dense are used in this account and are illustrated in Figure 6. Lax or moderately lax thyrses characterize sections *Amelina* and *Aneilema*, while moderately lax to dense inflorescences are typical of the remaining sections, the densest thyrses occurring in sections *Brevibarbata* and *Pedunculosa*. The larger thyrses—those more than 10 cm long—are always lax.

The cincinni have a basically alternate arrangement on the inflorescence axis. In some species, e.g., *A. aequinoctiale* and *A. johnstonii*, some or all of them may appear opposite or verticillate, but closer inspection and observations of their sequence of flowering reveal that they too are truly alternate. Therefore, such arrangements have been termed subopposite and subverticillate here. The three basic types of cincinnus arrangement are illustrated in Figure 7. Moderately lax to dense inflorescences usually have predominantly alternate cincinni; lax thyrses commonly have mainly subopposite or subverticillate cincinni. Not infrequently all three arrangements may occur within a single inflorescence.

Thyrses terminate the main shoots in nearly all *Aneilema* species. They are also terminal on lateral shoots of various lengths in most species. The lateral, inflorescence-terminated

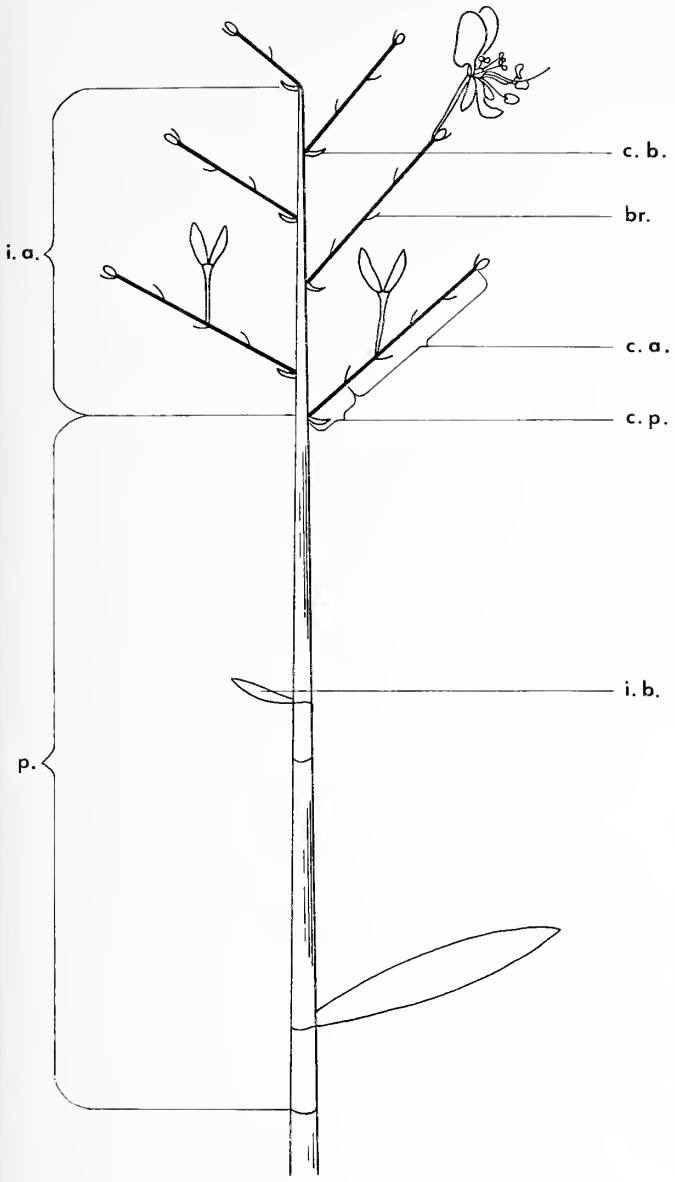


FIGURE 5.—Diagram of the structure of the *Aneilema* inflorescence (br. = bracteole, c.a. = cincinnus axis, c.b. = cincinnus bract, c.p. = cincinnus peduncle, i.a. = inflorescence axis, i.b. = inflorescence bract, p = peduncle).

shoots may be elongate and have normal foliage leaves, or abbreviated and bear only reduced leaves or bracts below the inflorescence. These shoots may perforate the sheaths or emerge from their mouths. Only *A. zebrinum* has strictly axillary inflorescences (Plate 4*g*).

The abbreviated, inflorescence-terminated, lateral shoots that bear only bracts or very reduced leaves below the inflorescence are the "cyme-branches" of Clarke (1901:73) and "inflorescence-shoots" of Forman (1962). These differ from strictly lateral inflorescences, according to Forman (1962), by having a basal prophyll. By applying that criterion, there are no truly lateral inflorescences in *Aneilema*, even in *A. zebrinum*, only inflorescence-shoots. However, it is questionable whether a special term like "inflorescence-shoot" is desirable for a condition that is merely one end of a continuous range of variation in size and development of these inflorescence-bearing shoots. Often the whole range may be found on a single plant. Furthermore, whether or not a basal prophyll is present—one may ask if the prophyll can ever be lost by reduction—the inflorescence is still a shoot system and it is still lateral.

From the above discussion it is obvious that the distinction among an inflorescence terminal on a lateral shoot, an inflorescence-shoot, and a lateral inflorescence derives partly from the length and degree of development of the shoot and partly as a matter of definition. In the present account, an "inflorescence terminal on a lateral shoot" is applied only to the leafy shoots that are normally produced at least several nodes below the terminal inflorescence of the main shoot. The terms lateral inflorescence and inflorescence-shoot have been used interchangeably for the very reduced inflorescence-terminated shoots that may be produced from leaf axils anywhere along the stem. The term secondary inflorescence has sometimes been employed for an inflorescence-shoot arising from the inflorescence bract.

Although inflorescence-shoots may be produced from any node in some species, e.g., *A. zebrinum* and *A. petersii* subsp. *pallidiflorum*, more commonly they are restricted to the uppermost few nodes below the terminal thyrse. Under these circumstances they usually form loose associations with that inflorescence. In a few species, e.g., *A. indehiscens* and *A. umbrosum*, the association of the terminal thyrse and lateral inflorescence-shoots is so close that the whole group may be treated as a larger inflorescence unit (Brenan, 1966). This is the *Synfloreszenz* of Troll (1961).

The uppermost leaf on the flowering shoot is often highly modified, always differing from the foliage leaf below it in size and sometimes in shape, texture, and pubescence. It varies from foliaceous and herbaceous to bract-like and membranous; its lamina is always sessile. In some species, e.g., *A. pedunculosum* and *A. spekei*, it completely encloses and protects the young, pre-flowering inflorescence. In *A. clarkei*, *A. succulentum*, and *A. lamuense*, it surrounds the inflorescence at all stages. In *A. petersii* subsp. *pallidiflorum* it is often erect and serves as a background for the white or whitish flowers (Plate 2*o*). In these species and others the uppermost leaf is clearly more of a reproductive structure than a vegetative one. For this reason it is called the inflorescence bract in this account. For consistency the same terminology has been applied to all *Aneilema* species, including those in which the uppermost leaf is not highly modified. Because the uppermost leaf is considered a reproductive structure, the peduncle, which is almost always present, is treated as the sum of the lengths of the two uppermost internodes below the inflorescence, i.e., the distance between the node of the second leaf below the inflorescence and the lowermost cincinnus (Figure 5). As in all Commelinaceae, the basic unit of the inflorescence in *Aneilema* is the cincinnus. The cincinnus has usually been considered a

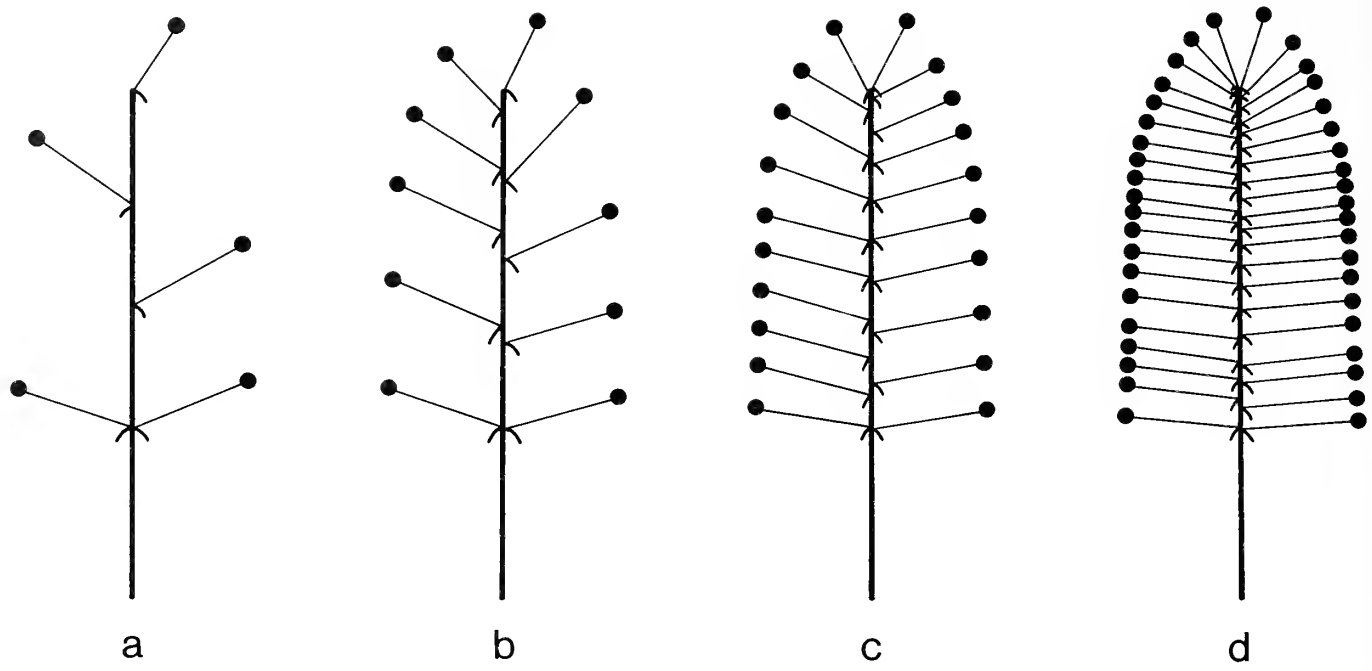


FIGURE 6.—Density of the *Aneilema* inflorescence: *a*, lax; *b*, moderately lax; *c*, moderately dense; *d*, dense.

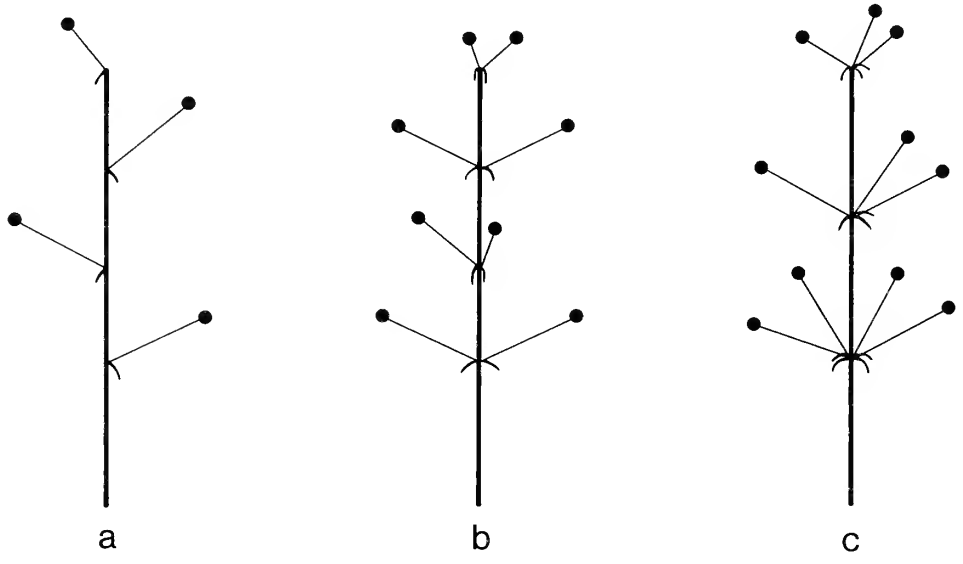


FIGURE 7.—Cincinnus arrangements in *Aneilema* inflorescences: *a*, alternate; *b*, subopposite; *c*, subverticillate.

scorpioid cyme (e.g., Brenan, 1966), but Lawrence (1951) has termed it a helicoid cyme, noting that such cymes are often mistakenly called scorpioid. It is beyond the scope of this discussion to determine whether the monochasial cymes in the Commelinaceae are helicoid or scorpioid: they will simply be called cincinni, as they have been by most authors.

Every cincinnus is subtended by a persistent bract, the cincinnus bract. Cincinnus bracts commonly have subapical glands that appear to be functional only in the very young, pre-flowering inflorescence. In some species of section *Pedunculosa* each cincinnus bract has a linear apex terminated by a clavate gland. In a few *Aneilema* species, e.g., *A. forskalii*, glands are sometimes present along the margins of the cincinnus bracts.

The cincinnus consists of a sympodial axis along which two ranks of bracteoles are arranged (Figure 8). The most basal internode of the cincinnus, that between the inflorescence axis and the first bracteole, is commonly much longer than the others and is called the cincinnus peduncle. (The term stipe has been used for this structure by Hunt (1986), but I prefer cincinnus peduncle because it is less ambiguous.) The remaining internodes collectively constitute the cincinnus axis. Both the cincinnus peduncle and axis are usually elongate, but in some species, the latter or both may be much abbreviated or suppressed. No species has very reduced cincinnus peduncles with elongate cincinnus axes. The number of flowers that will be produced by a cincinnus is essentially indeterminate, but it may regularly be few or even one in some species.

Persistent, pedicel-opposed bracteoles are present in all *Aneilema* species. They are usually amplexicaul and commonly cup-shaped and perfoliate. When amplexicaul they enclose and protect the cincinnus apex and young buds. In nearly all species every bracteole has a subapical gland. In a few taxa, e.g., *A. forskalii,* smaller glands are also present along the bracteole margin. Those species of section *Pedunculosa* that have cincinnus bracts terminating in clavate glands also have similarly shaped bracteoles. In the present account, bracteole length is considered the length of the bracteole midrib. For those species with perfoliate bracteoles, a second measurement, bracteole height, is the length of the fused edge.

The morphology of nearly all *Aneilema* inflorescences can be understood from the above discussion. The most highly reduced, specialized types require further comment. As noted above, all inflorescences of *A. clarkei* consist of solitary cincinni (Figure 9; Plate 3*p;* see discussion under *A. clarkei,* p. 133). These cincinni lack a peduncle and have a very contracted axis. Each cincinnus is subtended by and partially enclosed in a pair of generally leafy bracts, the outer, larger one the inflorescence bract, the inner the cincinnus bract. The somewhat spathe-like inflorescence bract is analogous to but not homologous with the spathe of *Commelina,* which is a cincinnus bract. Inflorescences of the type of *A. clarkei* also occur in *A. succulentum* and *A. lamuense* (Plate 4*e*).

The perforating inflorescence-shoots of *A. zebrinum* are similar to those of *A. clarkei* except that the inflorescence and cincinnus bracts are very reduced and the cincinnus is more elongate. Further variation in *A. zebrinum* is discussed under that species.

FLOWERS IN GENERAL.—The flower in *Aneilema* shows greater interspecific variation than any other organ. This variation is both biologically important, reflecting differences

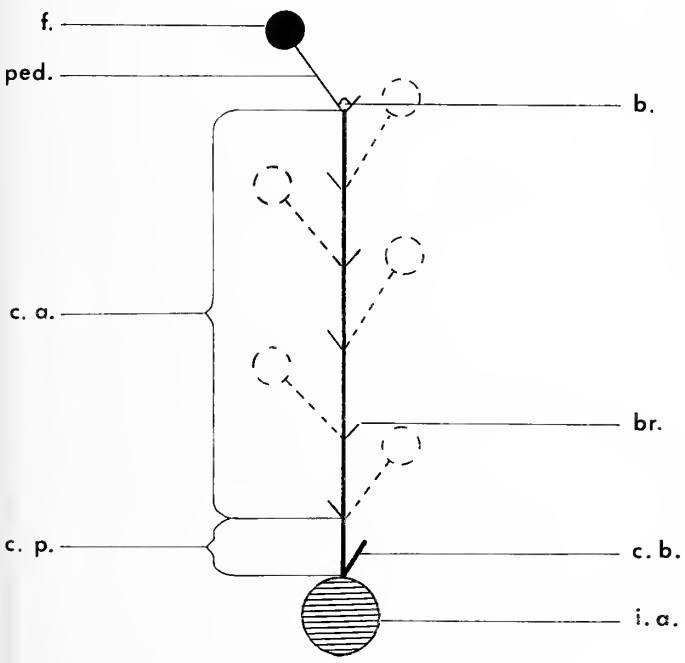


FIGURE 8.—Diagram of an *Aneilema* cincinnus. (The broken lines represent the positions of previous flowers; b. = bud, br. = bracteole, c.a. = cincinnus axis, c.b. = cincinnus bract, c.p. = cincinnus peduncle, f = position of flower, i.a. = inflorescence axis, ped. = pedicel.)

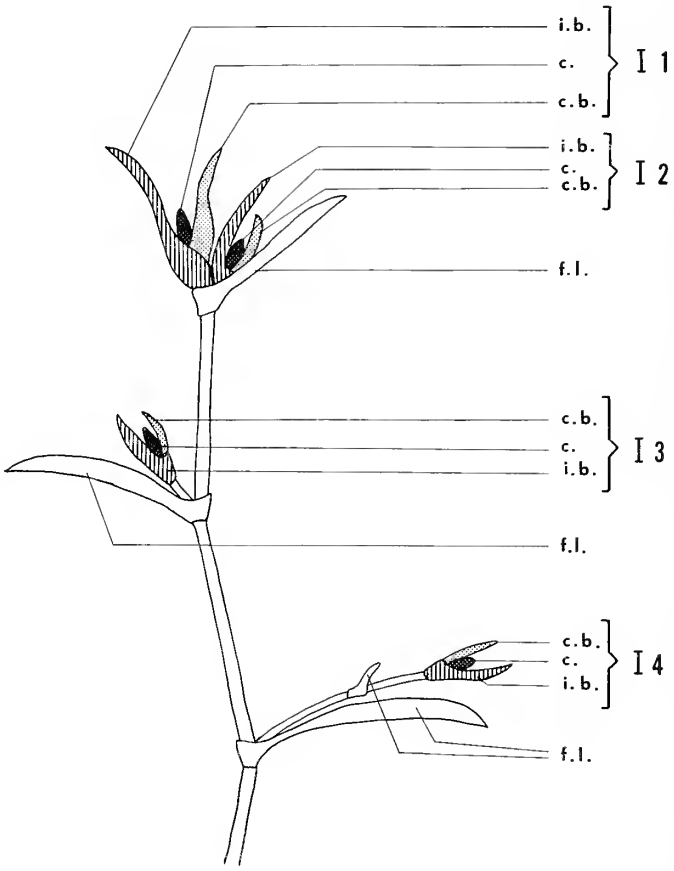


FIGURE 9.—Diagram of the distal end of a flowering shoot of *Aneilema clarkei* Rendle showing the position and structure of the inflorescences: I1 is the terminal inflorescence of the shoot; I2, I3, and I4 are terminal on short axillary shoots (c = cincinnus, c.b. = cincinnus bract, f.l. = foliage leaf, i.b. = inflorescence bract).

in breeding systems, including pollination mechanisms, and taxonomically useful, providing approximately as many characters as all the other organs combined. Floral characters also include the majority of attributes found useful for phylogenetic deductions. In previous studies of *Aneilema*, e.g., Clarke (1881a, 1901), Morton (1966), floral characters have not been given the emphasis they deserve, partly because they are difficult to interpret or often lacking in dried specimens and partly because their great variability within the genus as a whole has not been recognized. Flowers of 34 species of *Aneilema* are illustrated in Plates 1–4.

Aneilema flowers are borne in two ranks along the cincinni. They are pedicellate, pentacyclic, trimerous, and zygomorphic. Their basic structure consists of three free, sepaloid sepals, three free, petaloid petals, three staminodes (one antesepalous, two antepetalous) borne on one side of the flower, three stamens (two antesepalous, one antepetalous) borne on the other side, and a fundamentally trilocular ovary, in which one locule is frequently abortive (Figure 10). The flowers are generally unscented and remain open for a few daylight hours at the end of which they fade. Fading includes deliquescence of the corolla. Perfect, pistillate, and staminate flowers occur, the type or types present usually being species specific. Flowers vary in size from four to 40 mm wide.

The zygomorphic symmetry of *Aneilema* flowers is due primarily to the one-sided arrangement of the stamens and staminodes. More striking in most species is the differentiation of the corolla into two larger, often more brightly colored, clawed petals and a smaller, duller, sessile one. A less obvious zygomorphy is also present in the calyx: the medial sepal is always morphologically distinct from the lateral sepals. The plane of symmetry of the *Aneilema* flower bisects one member of each whorl: the medial sepal, medial staminode, dorsal locule of the ovary, medial stamen, and medial petal (Figure 10).

The flowers of most *Aneilema* species are regularly held horizontally, i.e., like a pea flower. In these species one can unambiguously refer to upper and lower sepals and petals. In *A. neocaledonicum* and *A. biflorum*, however, the flowers are primarily vertical, and the calyx and corolla members are best termed medial (or outer) and lateral (or paired or inner). For consistency, the terminology required for the vertical flowers has been applied to all species. The horizontal flowers characteristically have the medial sepal, paired petals, and staminodes on the upper side and the paired sepals, medial petal, and stamens on the lower side.

The terms outer and inner can be used for the sepals without confusion because, in bud, one sepal (the medial) always overlaps, i.e., is outside of, the other two sepals. Similarly, the medial petal in bud consistently overlaps the other two petals. The terms adaxial, abaxial, dorsal, ventral, anterior, and posterior, which are all defined with reference to an axis, have not been used for the sepals and petals, because they are ambiguous when applied to a flower that is morphologically terminal, and because they can readily be avoided.

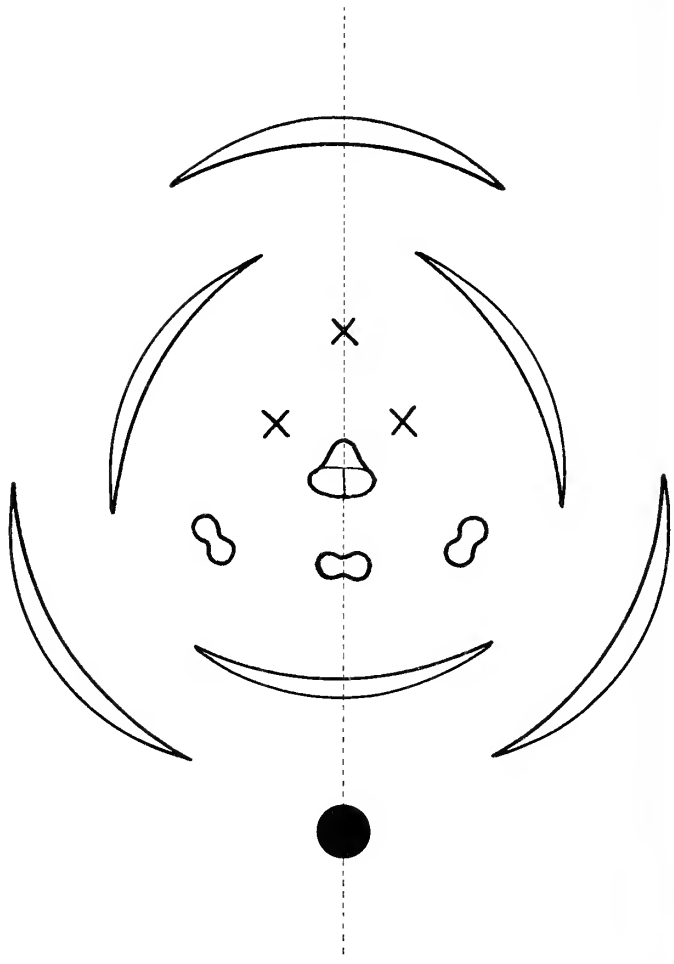


FIGURE 10.—Floral diagram of *Aneilema*. (The solid circle represents the cincinnus axis, the dotted line the plane of symmetry.)

The primary orientation of the flowers appears to be to gravity, not to other inflorescence structures. It has been observed in cultivation that when flowering shoots fall over, the flowers that are produced subsequently are still horizontal despite the change in position of the inflorescence. A reorientation of the buds occurs. This has been noted to happen in as few as 12 hours in *A. brenanianum*, but no experiments have been conducted.

Aneilema species may have only perfect, perfect, and staminate, or pistillate, perfect, and staminate flowers. When flowers of more than one type are present, they occur in the same inflorescences, and the plants are andromonoecious or polygamomonoecious. In andromonoecious and polygamomonoecious species the different types of flowers are produced in a characteristic sequence in new inflorescences: perfect then staminate flowers in the former; pistillate, then perfect, then staminate flowers in the latter (Figures 11–14). These sequences occur during the first few days of flowering in

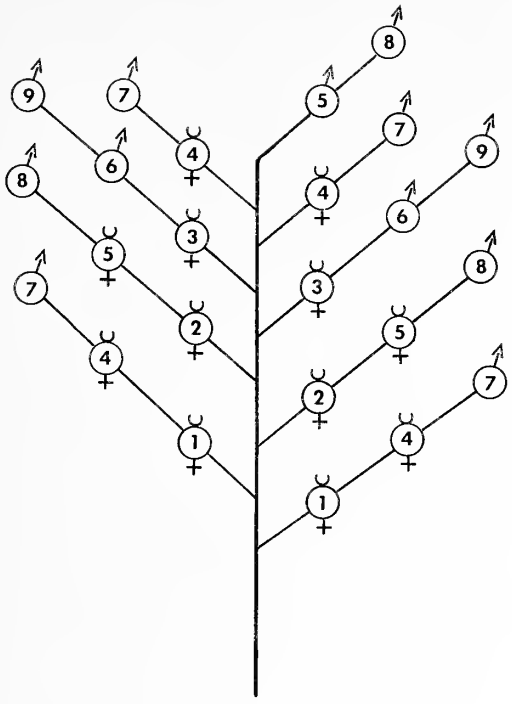


FIGURE 11.—Idealized flowering sequenee in an inflorescence of an andromonoecious *Aneilema* species: diagram of the inflorescence showing the distribution of perfect and staminate flowers over the first nine days of flowering. The numbers are the days in the flowering sequence on which particular flowers opened.

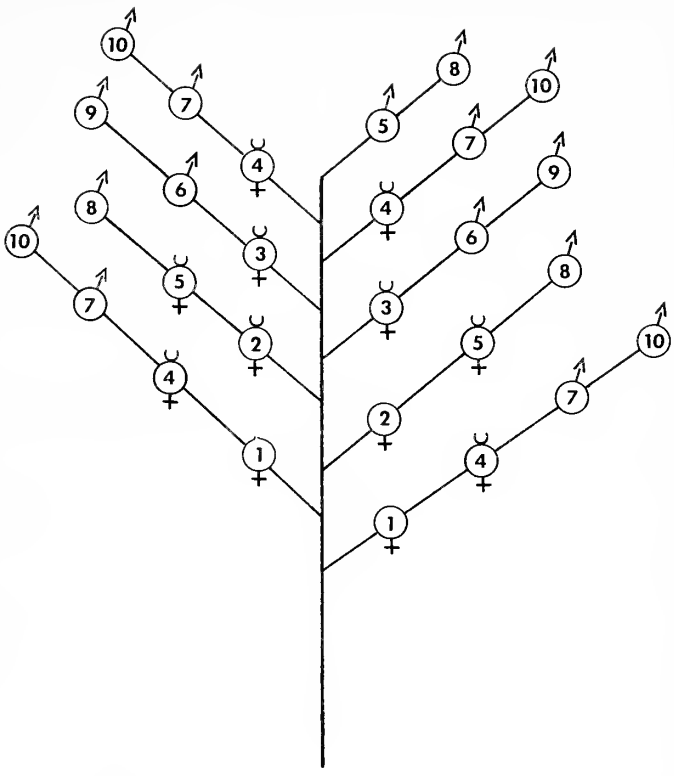


FIGURE 13.—Idealized flowering sequence in an inflorescence of a polygamomonoecious *Aneilema* species: diagram of the inflorescence showing the distribution of pistillate, perfect, and staminate flowers over the first 10 days of flowering. The numbers are the days in the flowering sequence on which particular flowers opened.

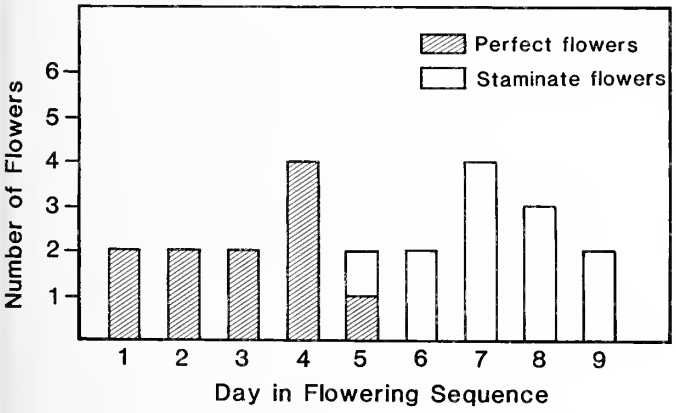


FIGURE 12.—Idealized flowering sequence in an inflorescence of an andromonoecious *Aneilema* species: graph of the numbers of perfect and staminate flowers produced on each day of the flowering sequence. The numbers of flowers are based on Figure 11.

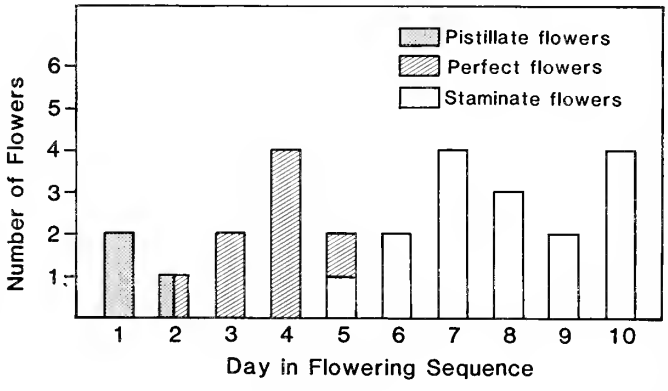


FIGURE 14.—Idealized flowering sequence in an inflorescence of a polygamomonoecious *Aneilema* species: numbers of pistillate, perfect, and staminate flowers produced on each day of the flowering sequence. The numbers of flowers are based on Figure 13.

an inflorescence. Flowers somewhat intermediate between two successive types, particularly pistillate and perfect, are sometimes produced. In older inflorescences the sequence is unpredictable, except that pistillate flowers almost never occur.

Few *Aneilema* species produce either solely perfect or all three types of flowers. Only perfect flowers are normally present in *A. arenicola, A. biflorum, A. neocaledonicum,* and *A. zebrinum* and in some populations of *A. beniniense*. Pistillate, perfect, and staminate flowers are regularly produced in populations of *A. hockii, A. somaliense,* and *A. welwitschii*. They have also been observed in populations of *A. leiocaule* and *A. macrorrhizum,* but the consistency of their occurrence in the last two species has not been established.

The majority of *Aneilema* species are andromonoecious. Staminate flowers in addition to perfect ones were first recorded in *Aneilema* by Kunth (1843) in *A. dregeanum* and have since been mentioned by Brückner (1930:163), Vogel (1955), Druten (1959), Brenan (1961), and Morton (1966). No author has indicated how widespread the occurrence of staminate flowers is in the genus. Brückner (1930:163) mentioned *Aneilema* merely as an example of a genus of Commelinaceae with staminate flowers; the other authors reported such flowers only in the context of their being present in certain *Aneilema* taxa.

Perfect and staminate (but not pistillate) flowers have been noted by the writer in the following *Aneilema* species: *acuminatum, aequinoctiale, beniniense* (some populations), *brenanianum, brunneospermum, calceolus, chrysopogon, clarkei, dispermum, dregeanum, ephemerum, forskalii, gillettii, hirtum, hockii* (some populations), *indehiscens* (all subspecies), *johnstonii, lamuense, lanceolatum* subsp. *lanceolatum, longicapsa, longirrhizum, minutiflorum, nicholsonii, nyasense* var. *brevisepalum, obbiadense, pedunculosum, petersii* (both subspecies), *pomeridianum, pusillum* (all subspecies but *gypsophilum*), *recurvatum, rendlei, schlechteri, sebitense, spekei, succulentum, tanaense, taylorii, termitarium, umbrosum, usambarense, woodii*. Because first flowers of inflorescences have not been seen in every case, a few of the above might ultimately prove to be polygamomonoecious rather than andromonoecious. Morton (1966) has reported perfect and staminate flowers in the additional taxa, *A. lanceolatum* subsp. *subnudum* and *A. setiferum*.

The distinction between andromonoecious and polygamomonoecious species in *Aneilema* is not always clean-cut. This is due to the first flowers in inflorescences of normally andromonoecious populations often having reduced anthers. It appears that certain environmental factors can cause the complete suppression of pollen production in these anthers. Under such circumstances the flowers are pistillate and the plant polygamomonoecious.

Great variation in the proportion of pistillate flowers has been noted in a population of *A. hockii* in Kenya (*Faden & Faden 74/227*), possibly in response to water availability. Under conditions of water stress there was much bud abortion, and 82% of the flowers were pistillate. During a normal rainy season no bud abortion was noted, and only 5% of the flowers were pistillate. Prolonged observations of *A. hockii* plants in cultivation suggest that the ratio of flowers of different types is also mediated by temperature extremes, but no experimental studies have been conducted.

The morphological differences between pistillate and perfect flowers on the one hand and between staminate and perfect flowers on the other often extend beyond the mere suppression of the stamens or the gynoecium. In *A. somaliense* and *A. welwitschii*, the pistillate flowers are smaller than the perfect flowers that follow them (Plate 2*f*). All three anthers are reduced and lack pollen. The filaments of the lateral stamens are very short.

The pistillate flowers of *A. hockii* (Plate 1*l*) also show a reduction in flower size and lateral stamen length. However, the medial stamen is fully developed and its anther polleniferous. These flowers are functionally pistillate because the pollen produced by the medial anther does not stain with cotton blue and is apparently sterile (Figure 15; Table 1, p. 32). These pistillate flowers of *A. hockii* further differ from the perfect ones in having shorter styles, larger stigmas, and, in at least one population, more ovules.

Brückner (1926:32) reported dimorphism in the staminodes of *A. beniniense*, but no such differences have been found in that or any other *Aneilema* species in the present study. Brückner's cultivated plants should therefore be considered exceptional.

In many andromonoecious or polygamomonoecious species, the lateral stamens are dimorphic in the staminate and perfect flowers. Stamen dimorphism has been observed by the writer in the following *Aneilema* species: *aequinoctiale, beniniense*

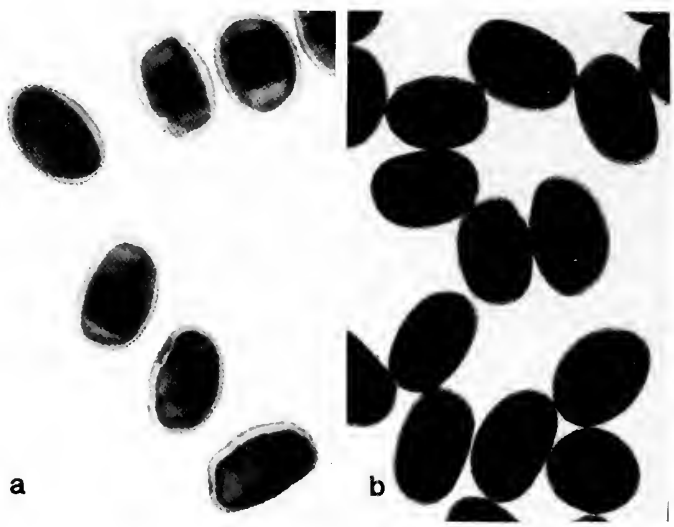


FIGURE 15.—Pollen grains of *Aneilema hockii* De Wildeman stained and mounted in cotton blue: *a*, medial anther pollen (×~300); *b*, lateral anther pollen (×~300). Both from *Faden et al. 72/234*.

(some populations), *brenanianum, gillettii, hockii, lamuense, longicapsa, rendlei, succulentum, taylorii* (some populations), *usambarense*. It should be expected to be found in other taxa, because no monoecious species has yet been proven not to have dimorphic stamens. However, detailed stamen measurements have not been made for any species that lacked conspicuous stamen dimorphism.

Dimorphic lateral stamens in staminate and perfect flowers always differ in filament length, the filaments being longer in the staminate than perfect flowers (Figure 16; Plates 1*g*, 2*b,d*). Differences only in length have been noted in *A. aequinoctiale, A. gillettii, A. hockii,* and *A. longicapsa*. Further differences may occur in filament curvature, divergence from the floral midplane, and in anther orientation. Filament divergence differences are usually manifested in the stamens of the perfect flowers being more divergent than those of the staminate flowers. This has been noted in *A. beniniense, A. brenanianum, A. rendlei,* and *A. taylorii*. Conversely, in *A. lamuense* and *A. succulentum*, the stamens of the staminate flowers are more divergent (Figure 28*c,d*). Dimorphism in stamen curvature occurs in *A. brenanianum* and *A. rendlei* and that in anther orientation only in the latter species (Plate 2*b,d*). The stamens of perfect and staminate flowers in *A. rendlei*, the most dimorphic stamens yet observed in any *Aneilema* species, are illustrated in Figure 17. The extent of the stamen dimorphism in *A. usambarense* has not been determined because no living or preserved flowers have been seen.

Another type of floral dimorphism reported in *Aneilema* is heterostyly (Vogel, 1955, 1978). Vogel's record of long- and short-styled flowers in *A. aequinoctiale* was undoubtedly based on a misinterpretation of flowers that were morphologically intermediate between perfect and staminate flowers. Such flowers have been observed occasionally in this species by the writer. They have well-developed styles that are shorter than those of the perfect flowers. They are functionally staminate, however, because their ovaries, although large, are not fully developed. This is not a case of true heterostyly, which is unknown in *Aneilema*. The suggestion by Ornduff (1974) that Vogel (1955) might have been referring to an androdioecious condition rather than to true heterostyly is also inaccurate; androdioecism does not occur in *Aneilema*. As noted above, *A. aequinoctiale* is andromonoecious.

The styles of many species may curve out of the floral midplane, either to the right or to the left (Plates 2*n,p*, 3*a,b,d,g,k,l,n*, 4*d*, and see below). This does not constitute true enantiostyly because there are no differences in stamen curvature in right-styled or left-styled flowers.

A distinct but weak fragrance has been noted in the flowers of *A. brenanianum, A. brunneospermum, A. hockii, A. johnstonii* (some populations), *A. longirrhizum, A. nicholsonii, A. rendlei,* and *A. somaliense*. Among these species, the strongest scents are in *A. hockii, A. longirrhizum, A. rendlei,* and *A. somaliense*. A possible scent was recorded in one population of *A. dregeanum* subsp. *dregeanum*. The fragrances

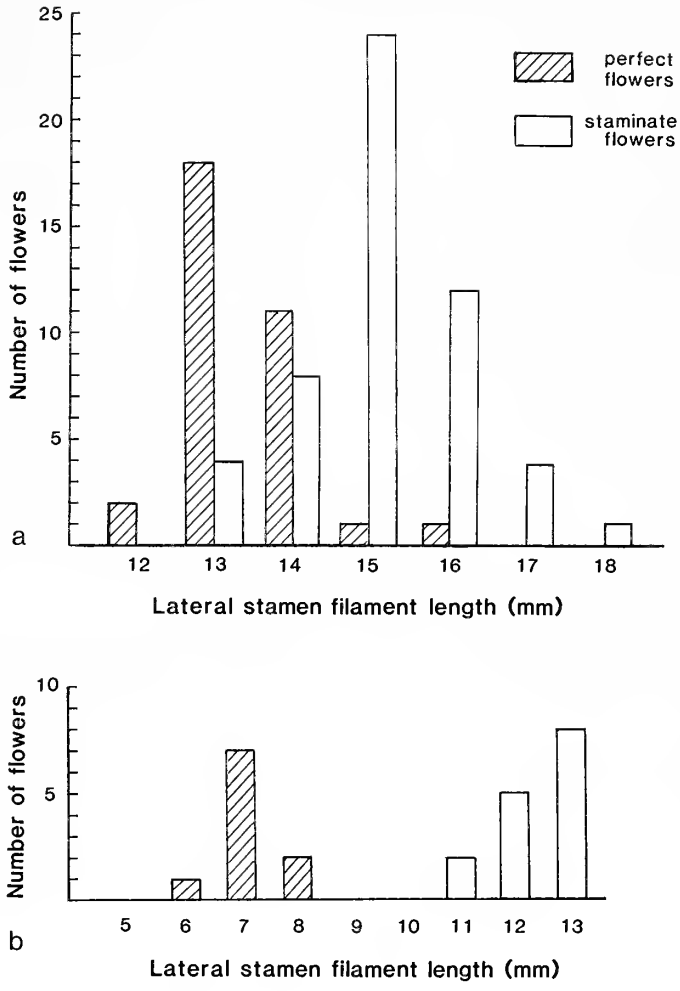


FIGURE 16.—Lateral stamen filament lengths in perfect and staminate flowers of two *Aneilema* species: *a, A. aequinoctiale* (P. de Beauvois) G. Don, collective data from several days (from *Faden et al. 71/922*); *b, A. rendlei* C.B. Clarke, data from one day (from *Kabuye & Evans 163*). The data are from single plants in cultivation.

have not been characterized chemically. No odors could be detected in approximately 25 species.

The corolla and calyx in *Aneilema* buds have an imbricate aestivation. As a result, the sepals and petals can be numbered following Eichler (1875): 1, outer, overlapping the other two; 2, middle, overlapping one, overlapped by the other; 3, inner, overlapped by the other two. Sepal 1 and petal 1 are the medial sepal and petal from the standpoint of floral symmetry.

Two types of aestivation of the inner petals have been found in *Aneilema* buds (Figure 18). In Type I (Figure 18*a*), petal 2 overlaps petal 3 on the side of the flower towards the outer sepal. Petal 3 overlaps petal 2 on the opposite side of the flower. In the Type II arrangement (Figure 18*b*), petal 2 completely envelops petal 3. Both types of arrangement have been found in approximately equal numbers in inflorescences of *A. hockii* and *A. taylorii*. Only Type I was found in 10 buds

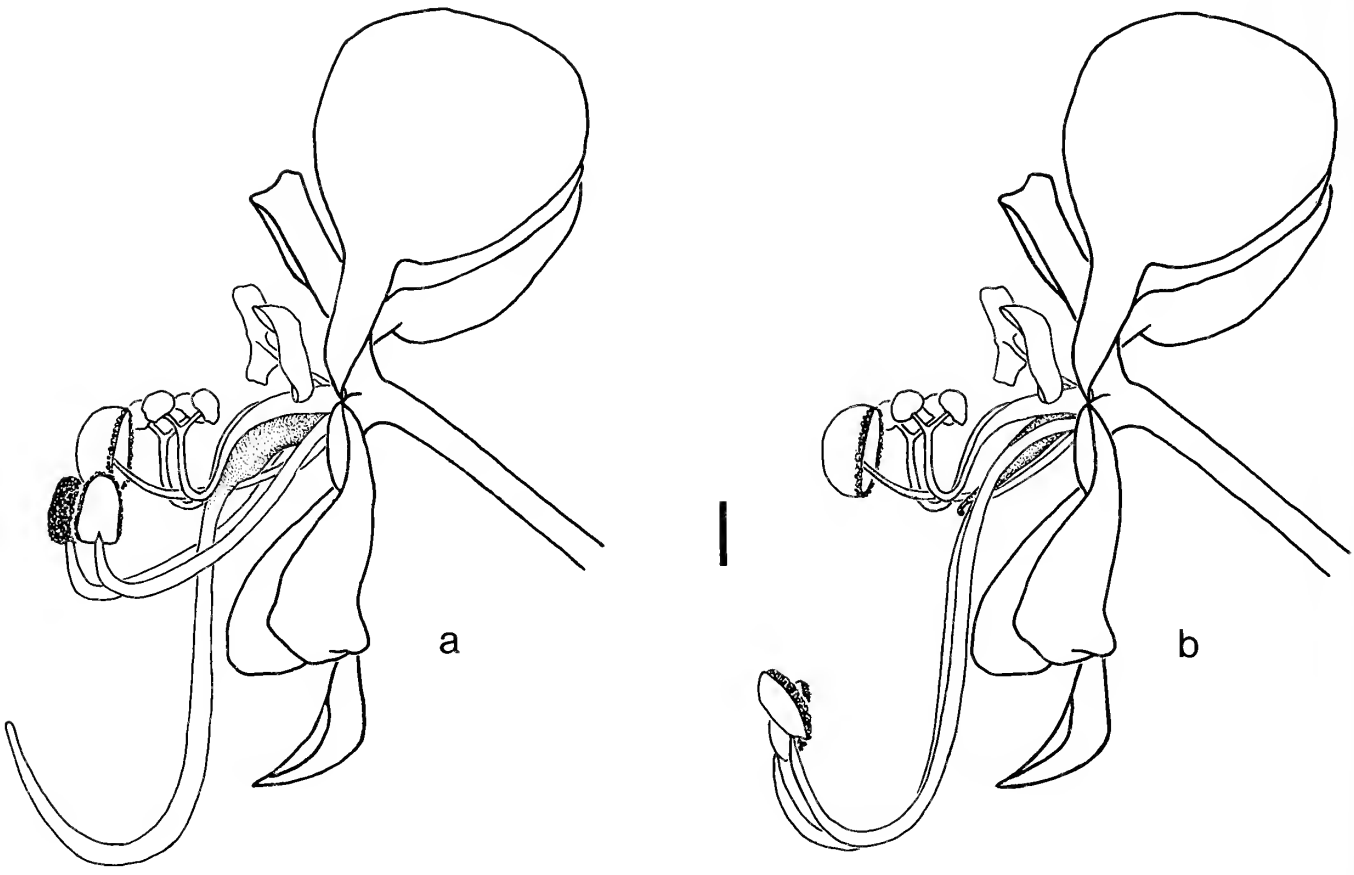


FIGURE 17.—Perfect and staminate flowers in *Aneilema rendlei* C.B. Clarke: *a*, perfect flower, side view; *b*, staminate flower, side view (from *Kabuye & Evans 163*). (Bar = 1 mm.)

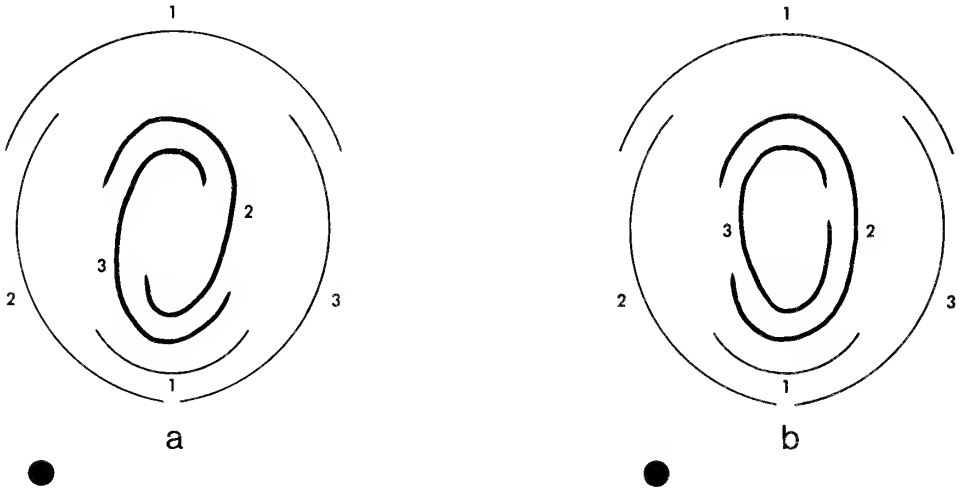


FIGURE 18.—Lateral petal aestivation types in *Aneilema: a*, Type I: petal 2 and petal 3 mutually overlapping; *b*, Type II: petal 2 enveloping petal 3 (the solid circles represent the cincinnus axis). Both from *A. hockii* De Wildeman (*Faden & Evans 71/502*).

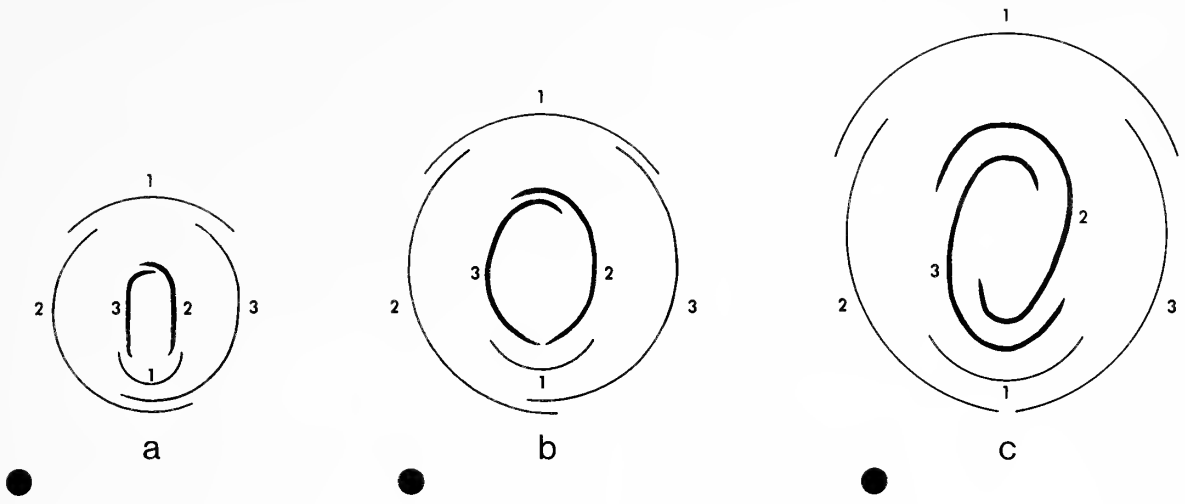


FIGURE 19.—Lateral petal aestivation development in *Aneilema: a*, petal 2 overlapping petal 3 dorsally, no overlap ventrally; *b*, petals 2 and 3 meeting in a valvate fashion ventrally; *c*, petal 3 overlapping petal 2, resulting in a Type I arrangement. The solid circles represent the cincinnus axis. All from *A. hockii* De Wildeman (*Faden & Evans 71/502*).

of *A. umbrosum* subsp. *umbrosum*. The taxonomic significance of these differences, if any, is unknown.

The distribution of the two petal aestivation types within the inflorescence has been investigated in *A. hockii*. An inflorescence of 12 cincinni was found to have a Type I arrangement in the largest buds of six cincinni and a Type II arrangement in the equivalent buds of the other six cincinni. In five of the cincinni, it was possible to check two successive buds for petal arrangement. In three of these cincinni, successive buds had the same type of petal aestivation; in the other two, sequential buds had different petal aestivation types. No pattern to the distribution of the petal aestivation types could be found within the inflorescence. The characters considered were bud size, position on the cincinnus, and cincinnus position in the inflorescence.

The random distribution of the two petal arrangements in buds of *A. hockii* could be understood when buds of different sizes were examined (Figure 19). It was found that the overlap of petal 3 by petal 2 on the side towards sepal 1 was completely predictable and develops long before any overlap occurs on the opposite side of the flower (Figure 19*a*). At a later stage the as yet non-overlapping petal margins meet lengthwise in a valvate fashion (Figure 19*b*). At this point it appears to be a matter of chance as to which petal grows over the other.

The same pattern of development may be expected in *A. taylorii*, which is more difficult to work with than *A. hockii*, not only because of its smaller bud size, but also because the inner petals tend to spring apart when the outer one is rolled back. Furthermore, it appears that in many of the largest buds, the inner petals do not overlap at all on the lower ventral side (the reason that they spring apart?). In *A. umbrosum* subsp. *umbrosum*, it may be predicted that the lower edge of petal 3 turns inwards before this petal meets petal 2. Therefore, the edge of petal 2 always passes over that of petal 3 and a Type II arrangement regularly occurs.

A further variation is that petal 2 may be either on the right or left side, viewing the bud from the front. The position of petal 2 depends upon in which of the two floral ranks of the cincinnus the bud is located. When the bud is in the right rank (viewing the cincinnus from the apex) petal 2 is on the right and petal 3 on the left. A bud in the left rank of the cincinnus has its petal 2 on the left and petal 3 on the right. Thus petal 2 is always oriented away from the cincinnus axis and petal 3 towards it. Conversely, sepal 2 is always inclined towards the cincinnus axis and sepal 3 away from it (Figure 20). Because buds are produced alternately in the two ranks of the cincinnus, successive flowers always have mirror image symmetry with regard to the position of petals 2 and 3 and sepals 2 and 3.

The first flower of the cincinnus may be produced in either rank. Although the cincinni have a basically alternate arrangement on the inflorescence axis, no regular alternation of the rank of the first flower in successive cincinni has been found. Thus a cincinnus following one that had had its first flower in the left rank is just as likely to begin flowering in the same rank as in the opposite one.

No wholly satisfactory method of measuring flower size has been found. Flower width, the distance between the outer margins of the paired petal limbs, has been used here because of its ease of measurement. However, this distance is a function not only of the size of the paired petals but also of the angle at which they are held. Flowers in which the paired petals overlap each other will measure smaller than flowers that have non-overlapping petals of the same size. Furthermore, the angle at which the petals are held can vary depending upon whether

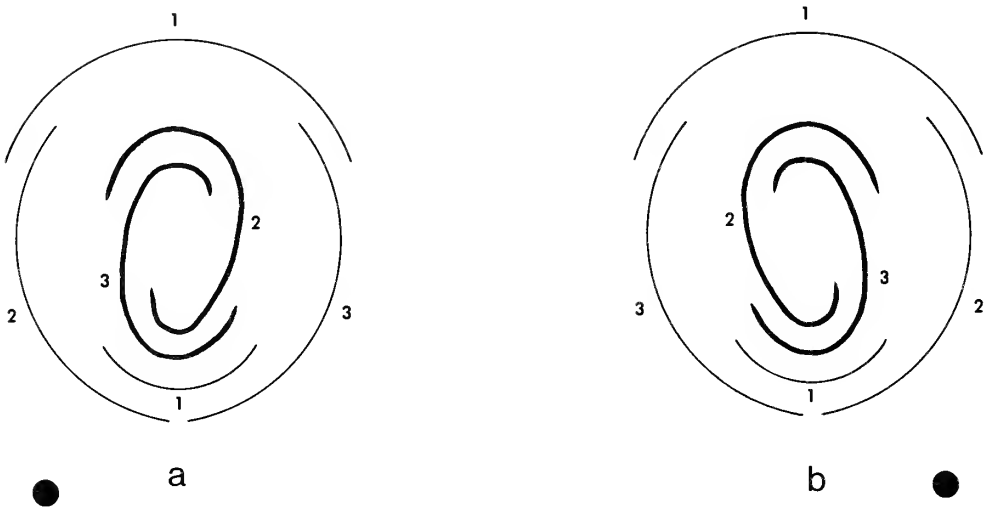


FIGURE 20.—Mirror image symmetry in *Aneilema* buds: *a*, bud from the right floral rank on the cincinnus; *b*, bud from the left floral rank on the cincinnus. The cincinnus is viewed from the apex. The solid dots represent the cincinnus axis. Both buds have a Type I aestivation. Both from *A. hockii* De Wildeman (*Faden & Evans 71/502*).

the flower is just opening, fully open, or beginning to fade. For standardization, measurements of flower width have been made from fully open flowers, whenever possible.

Within a species, flower size and hence flower width can be a function of the stage in the life cycle of the plant when measurements are made. The first flowers of inflorescences are usually smaller than later ones, and the last flowers produced by a plant, particularly an annual, are often diminutive. In the species descriptions the total range of flower widths measured in the field and in cultivation have been included.

PEDICELS.—Pedicels in *Aneilema* species vary in length, thickness, color, pubescence, curvature, and persistence. All except thickness and to a large extent color are useful taxonomically. Pedicel length usually increases measurably in fruit. The length by which the longest fruiting pedicel exceeds the longest flowering pedicel has been indicated in the species descriptions. Where no such difference has been noted, e.g., in *A. tanaense*, it is assumed that additional material would include longer fruiting pedicels than have yet been found. Flowering pedicels are generally aligned with the axes of the cincinni, i.e., horizontal to ascending. In the event of pollination and fruit set—and often even if they do not occur—the pedicel orientation changes, in order that there may be room for elongation of the cincinnus for the production of successive flowers. The pedicel may curve upward and backward (recurved), downward (decurved) or laterally. Curvature may occur along the whole length of the pedicel or chiefly at the base and/or apex. The various types of fruiting pedicel curvature in *Aneilema* are shown in Figure 21.

The overwhelming majority of *Aneilema* species have recurved fruiting pedicels. Most commonly the capsules are held erect or further inclined towards the inflorescence axis. Further recurvature occurs in most species of section *Lamprodithyros* and in a few taxa belonging to other sections. The method used to designate the angle of recurvature is shown in Figure 22.

Other fruiting pedicel curvatures are uncommon in the genus. Decurved pedicels, which always result in the capsules pointing downward, occur only in *A. biflorum*, *A. neocaledonicum*, *A. umbrosum* (both subspecies), and *A. taylorii* (frequently). Laterally spreading pedicels have been observed in *A. acuminatum*, *A. nyasense*, and *A. taylorii*.

The pedicels of flowers that do not set fruit abscise at their bases within a few days after flowering. However, fruiting pedicels in almost all *Aneilema* species persist even after the capsules have dehisced and the seeds have been shed. The only definite exception is *A. umbrosum* (both subspecies), in which the pedicels often abscise at the base about the time of capsule dehiscence. The fruiting pedicels of *A. biflorum* are also easily detached at the base when the seeds are mature; some of the pedicels and their attached capsules may therefore be naturally deciduous like those of *A. umbrosum*.

CALYX.—The calyx in *Aneilema* consists of three free, persistent, herbaceous, convexo-concave, sepaloid sepals. They are almost always distinctly glandular near the cucullate apex. The medial sepal always has bilateral symmetry; the lateral sepals are individually asymmetric, but they have mirror image symmetry. In addition to the difference in symmetry, the medial sepal commonly differs from the lateral sepals in being more deeply convexo-concave with a more strongly hooded apex, more prominently glandular and narrower. Differences in venation and distribution of pubescence are also frequent. All three sepals usually become appressed to the young capsule; they generally do not become reflexed. The sepal characters

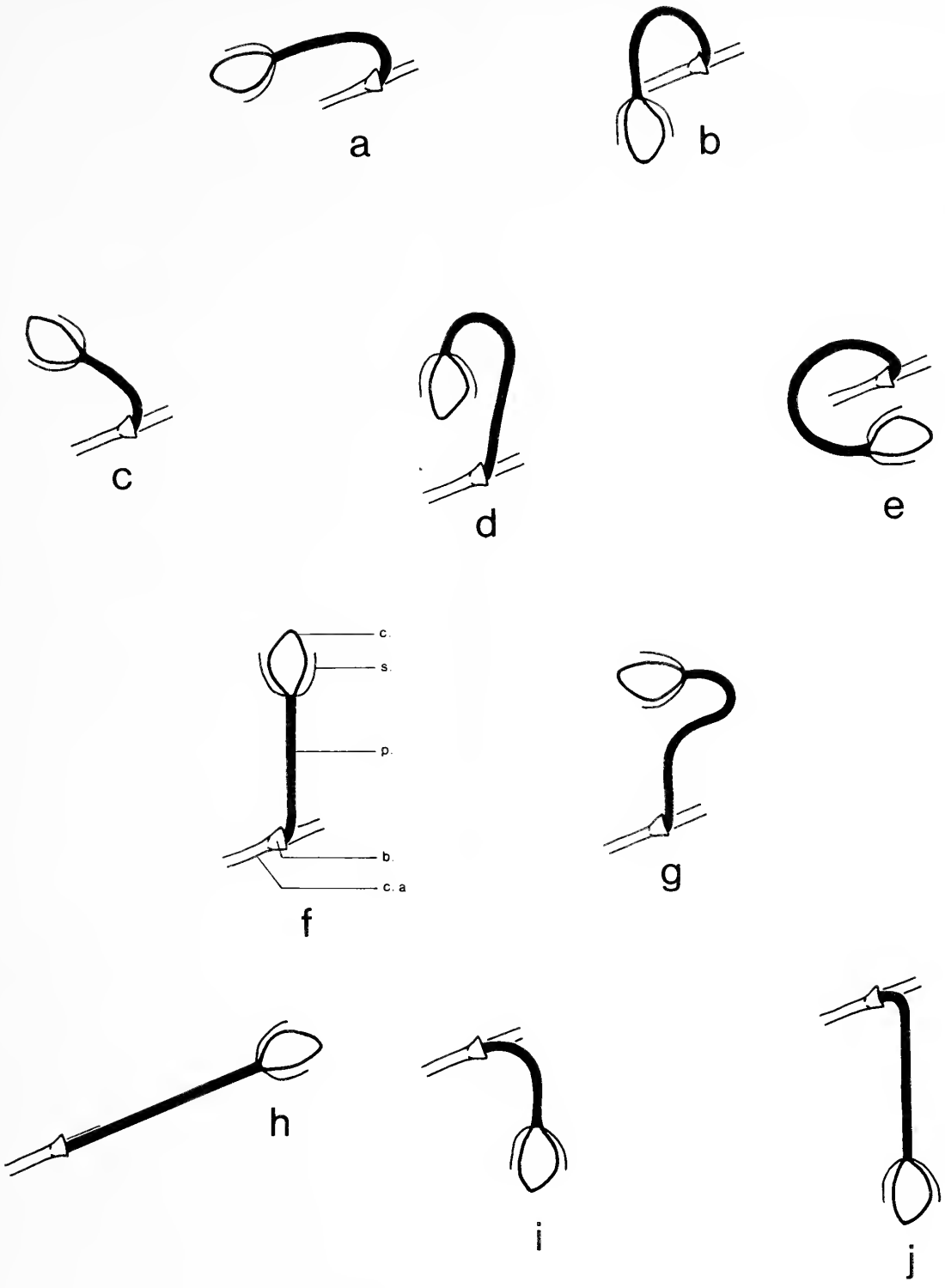


FIGURE 21.—Fruiting pedicel curvature types in *Aneilema: a–e, g,* recurved; *f,* erect; *h,* spreading laterally; *i,j,* decurved. The cincinnus apex is to the right. Examples of each type are *a, A. petersii* (Hasskarl) C.B. Clarke; *b, A. longirrhizum* Faden; *c, A. welwitschii* C.B. Clarke; *d, A. clarkei* Rendle; *e, A. tanaense* Faden; *f, A. rendlei* C.B. Clarke; *g, A. succulentum* Faden; *h, A. nyasense* C.B. Clarke; *i, A. umbrosum* (Vahl) Kunth; *j, A. neocaledonicum* Schlechter. (Not to scale; b = bracteole, c = capsule, c.a. = cincinnus axis, p = pedicel, s = sepal.)

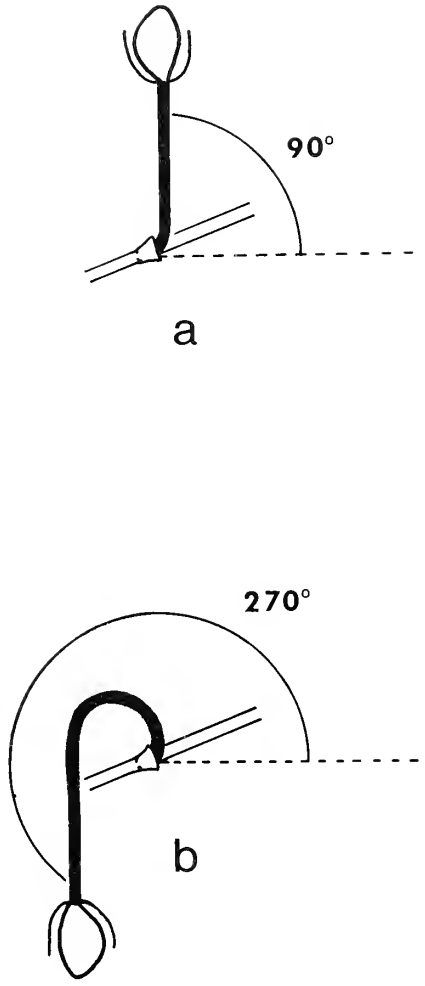


FIGURE 22.—Method of designating the angle of curvature in recurved *Aneilema* fruiting pedicels. The flowering pedicel is considered horizontal (except in *A. biflorum* R. Brown and *A. neocaledonicum* Schlechter, in which it is vertical), so that in *a*, an erect fruiting pedicel is recurved 90°; in *b*, a downward pointing pedicel is recurved 270°.

that are of taxonomic use are size, shape, color, prominence and distribution of glands, pubescence, and probably venation.

The convexity of the sepals makes their actual or curvilinear dimensions very difficult to measure. As a result linear dimensions have been used instead. The sepals have been measured as if they were planar figures.

The sepals are always partly or wholly green. Commonly the margins are transparent and may be tinged with various shades of purple or violet. In several species, e.g., *A. hockii, A. rendlei,* and *A. somaliense* (Plates 1*h,o,* 2*d,f,g*), the colored portions are more extensive and may form distinctive patterns with the green parts, e.g., alternating lengthwise stripes. In these species the sepals appear to constitute a significant part of the visual floral attraction to pollinators. The presence or absence of non-green areas on the sepals is sufficiently constant in most species to be useful taxonomically.

The major function of the sepals is protection of the inner floral whorls in bud. Protection against desiccation is provided by the secretion of the subapical sepaline glands. These vary from inconspicuous and unlobed to very prominent and distinctly bilobed (e.g., Plates 3*e,f,k,l,* 4*j,k,n–p*); rarely they appear to be completely lacking in some or all of the sepals, e.g., in *A. succulentum* and *A. zebrinum*. In many species the gland of the medial sepal is bilobed while that of the lateral sepals is unlobed. In *A. benadirense* and *A. tanaense*, small, marginal glands are present on the medial sepal in addition to the larger, subterminal gland.

Sepal pubescence probably also serves a protective function. Glandular microhairs, which are present on the adaxial surface of the sepals of all 27 *Aneilema* taxa in which this character has been checked, together with the sepaline glands, keep the inner floral parts and young fruit from desiccating. Other hair types present abaxially are two-celled hook-hairs, prickle hairs, and uniseriate, acicular hairs (Figure 40). Their distribution in 19 *Aneilema* species representing all seven sections of the genus is shown in Table 3 (p. 47). Such hairs may discourage feeding by herbivorous insects.

The sepals have three to about seven parallel veins, the larger of which converge at the subapical glands. None reaches the margin. A small number of cross veins are usually present. The venation pattern of the sepals may prove useful taxonomically, but no detailed investigations have been conducted.

COROLLA.—The corolla in *Aneilema* is composed of three free, deliquescent, petaloid petals: two equal, clawed, lateral petals, usually oriented upwards, and a morphologically distinct medial petal generally inclined downwards. The medial petal generally differs from the lateral petals in size, shape, color and lack of a claw. In sections *Aneilema* and *Lamprodithyros,* it is subequal to and usually concolorous with the paired petals (Plates 1*a–c,* 2*m–p,* 3*a–h,j–l,n–p,* 4*c–h*). In other sections it is always greatly reduced and generally dull colored relative to the paired petals. However, in *A. gillettii* (Plate 1*e,f*) the three petals are concolorous; in *A. hirtum* and *A. chrysopogon* (Plate 4*n,o*), the medial petal, although reduced and largely dull, has a conspicuous, subapical maroon spot; in *A. minutiflorum* all three petals are very reduced and thus secondarily subequal. The degree of differentiation between the medial and lateral petals as well as details of size, shape, and color of both are taxonomically useful.

The paired petals are usually planar, although the limbs may be reflexed at anthesis. In a few species, e.g., *A. johnstonii* and *A. longirrhizum* (Plate 1*d,k*), the apex of the limb is slightly hooded. The limb varies from elliptic or suborbicular to subdeltate, but most commonly it is ovate or broadly ovate. The limb apex is normally rounded to obtuse, but it may frequently or occasionally be acute or truncate to slightly emarginate in some species. The limb base varies from more or less symmetric to strongly asymmetric and from cuneate to cordate. In the asymmetric types, the medial side (side towards the floral midplane) is more narrowly cuneate than the lateral side, or

cuneate versus truncate, or truncate versus cordate to subcordate. The limb margins are entire to crenulate.

The limbs range in color from white to lilac, lavender, or rarely blue (but never the clear, sky blue of *Commelina* species), or very rarely red or from yellow to orange. The white to blue color range is the more common, occurring in all sections of the genus. A single population of *A. pusillum* subsp. *pusillum* (Plate 2*i,j*) has been noted with red flowers. Yellow to orange petals are infrequent in *Aneilema*, as they are in all other genera of Commelinaceae in which they occur: *Coleotrype, Commelina, Floscopa,* and *Murdannia.* In *Aneilema* they are present only in some species of sections *Amelina* (*aequinoctiale, ephemerum, johnstonii, nyasense*) and *Brevibarbata* (*angolense, homblei, macrorrhizum, welwitschii*) (Plates 1*d,i,j,* 4*j*).

Generally the entire limb is uniform in color. In *A. rendlei,* however, the veins are contrastingly dark compared to the background color. In some populations of *A. hockii,* the base of the limb is white, contrasting with the rest which is lavender. Petal luster is caused by reflectance from the facets of pyramidal epidermal cells on the adaxial surface of the limbs.

The claws are either concolorous with the limbs or paler than them. Like the limbs, they are usually glabrous, but in *A. aequinoctiale* (Plate 1*i*) and *A. ephemerum,* they are inconspicuously bearded with a mixture of glandular hairs and hook-hairs (Figure 40; Table 4, p. 48). Elsewhere in the Commelinaceae, petaline hairs have been reported only in *Cochliostema* and *Geogenanthus,* in both of which they are marginal. They have also been observed by the writer on the petal bases of *Murdannia simplex* in Ghana, Kenya, and Zambia.

The medial petal may be planar, but it is generally slightly to strongly convexo-concave. In section *Lamprodithyros,* it is large and cup-, boat- or slipper-shaped (Figures 23, 24; Plates 2*m-p,* 3*a-h,j-l,n-p,* 4*c-h*). In most species of this section, it retains the lateral stamens for some time after the flower opens (Plate 3*c,d,k,l*). The stamens are held by the involute margins of this petal and are released only when these margins uncurl, not through the action of pollinators. The stamens may be caught for a period of only a few minutes or up to nearly three hours, the mean length of time for which they are held being species specific (Figure 25). The stamen-retention mechanism is part of a pollination system, which is discussed in Faden (1983b) and below. The reduced medial petals of the other sections are often green-tinged, a color not found in the paired petals. The medial petal is glabrous in all species examined except *A. ephemerum* in which hairs, identical to those of the paired petal claws, are present at the base.

All three petals have three traces at the base. The medial trace usually remains unbranched for most of its length, ultimately dividing a few times near the petal apex. In some flowers of *A. petersii,* it may branch much more. The lateral traces remain more or less parallel to the medial trace for most of their length, giving off numerous branches unilaterally. These side veinlets fork repeatedly as they approach the margin (see Brenan, 1952:191, fig. 5). Anastomoses occur occasionally. None of the veinlets reaches the margin. This venation pattern shows little variation between species and is therefore not useful taxonomically.

Paired petal dimensions have been measured curvilinearly, except that the length of the hooded apex, in those species having one, has been excluded. Like the sepals, the medial petal has been measured linearly when it is not planar and cannot be flattened. An additional measurement, depth, has been used for the species in section *Lamprodithyros.* The width of the medial petals of these species is measured after the margins have fully unrolled. Medial petal shape, the linear outline when viewed from the front, is also recorded when the margins are fully extended in section *Lamprodithyros* species.

ANDROECIUM.—The androecium consists of three staminodes opposite the lateral petals and medial sepal (the antesepalous one occasionally lacking) and three stamens opposite the lateral sepals and medial petal. Thus the outer, antesepalous androecial whorl contains two stamens and a staminode, and the inner, antepetalous whorl two staminodes and a stamen (Figure 10). The usually horizontal orientation of the flowers results in the shorter staminodes being held above the longer stamens. The staminode and medial stamen filamants are always glabrous; the lateral stamen filaments are glabrous or variously bearded, according to the species. All of the filaments are usually free, except in section *Lamprodithyros,* in which those of the three stamens are always fused basally and frequently also shortly adnate to the filaments of the lateral staminodes (Figures 26-28; Plate 4*b*). A further short adnation to the medial petal base is also general in these species. In the remainder of the genus, fused stamen filaments have been observed only in *A. hockii* (section *Amelina*).

Staminodes: The medial staminode is usually differentiated from the lateral staminodes in size and form. Its filament is generally shorter and its antherode either larger or smaller and frequently with differently shaped lobes. The medial staminode is completely lacking or vestigial in the following *Aneilema* species: *benadirense, beniniense* (some populations), *calceolus, clarkei* (occasional flowers in some populations), *minutiflorum, setiferum* (sometimes lacking, fide Morton, 1966), *tanaense, termitarium,* and *umbrosum* (some populations). All three staminodes are equal or subequal in species of section *Aneilema* and in *A. johnstonii* (section *Amelina*) (Plate 1*a,c,d*).

Although sometimes distinctly thickened basally, the staminode filaments are always more slender than those of the stamens. Except in section *Rendlei* and in some populations of *A. hockii,* the staminode filaments are little curved, being straight or gently arcuate for all or most of their length (e.g., Plates 1*c,i,j,* 3*c,d,o,p,* 4*b,c,f*). The lateral staminode filaments are sometimes sharply deflexed near the apex. The strongly curved lateral staminode filaments of *A. rendlei, A. brenania-*

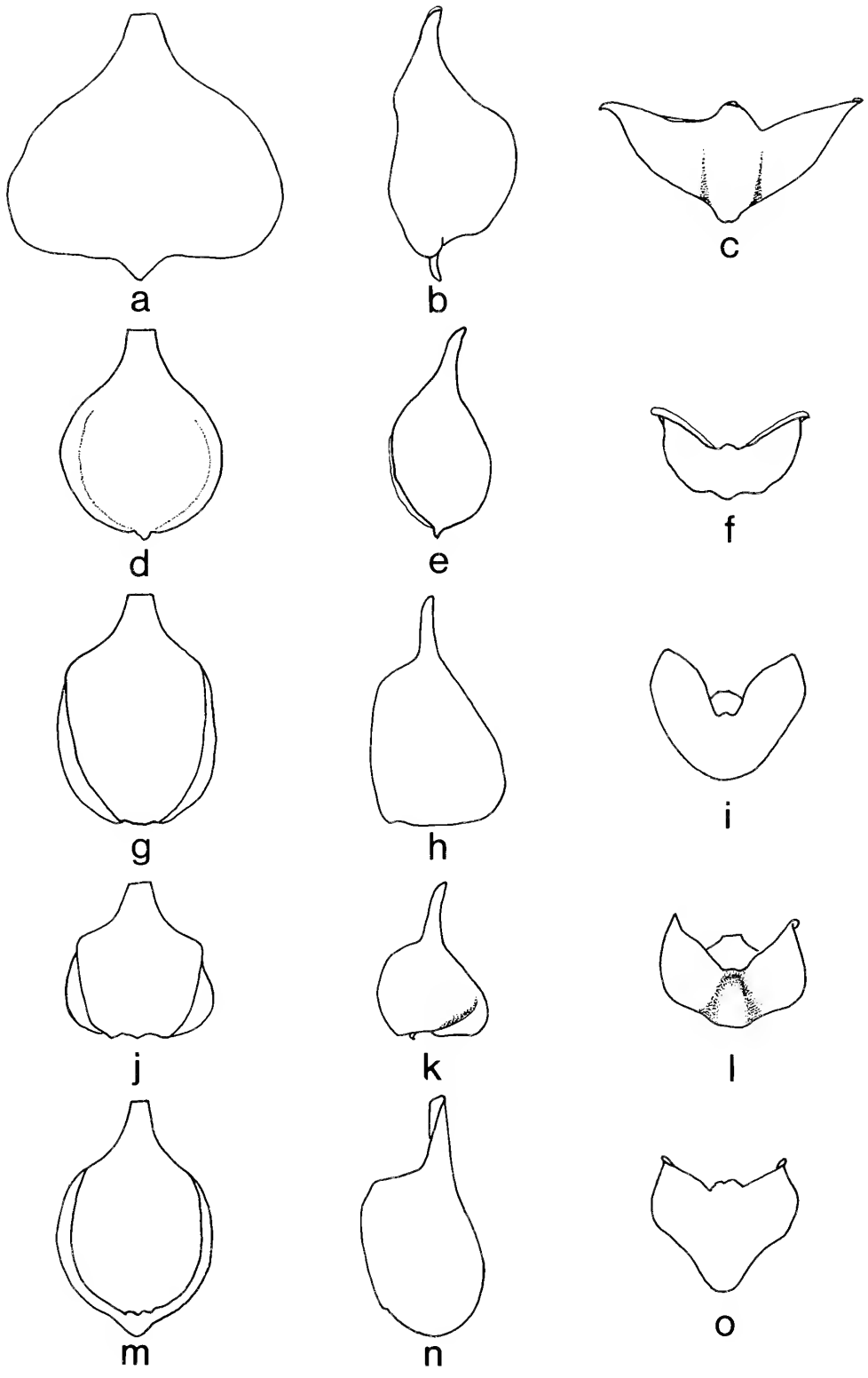


FIGURE 23.—Medial petals of five species of *Aneilema* section *Lamprodithyros: a–c, A. petersii* (Hasskarl) C.B. Clarke subsp. *petersii* (from *Andrews s.n.*); *d–f, A. indehiscens* Faden subsp. *indehiscens* (from *Faden & Faden 72/72*); *g–i, A. recurvatum* Faden (from *Faden 69/1300*); *j–l, A. tanaense* Faden (from *Gillett 19973*); *m–o, A. calceolus* Brenan (from *Organ in EA14970*). All are after stamens have been released (where appropriate). (*a,d,g,j,m,* front views; *b,e,h,k,n,* lateral views; *c, f,i,l,o,* apical views). (Bar = 1 mm.)

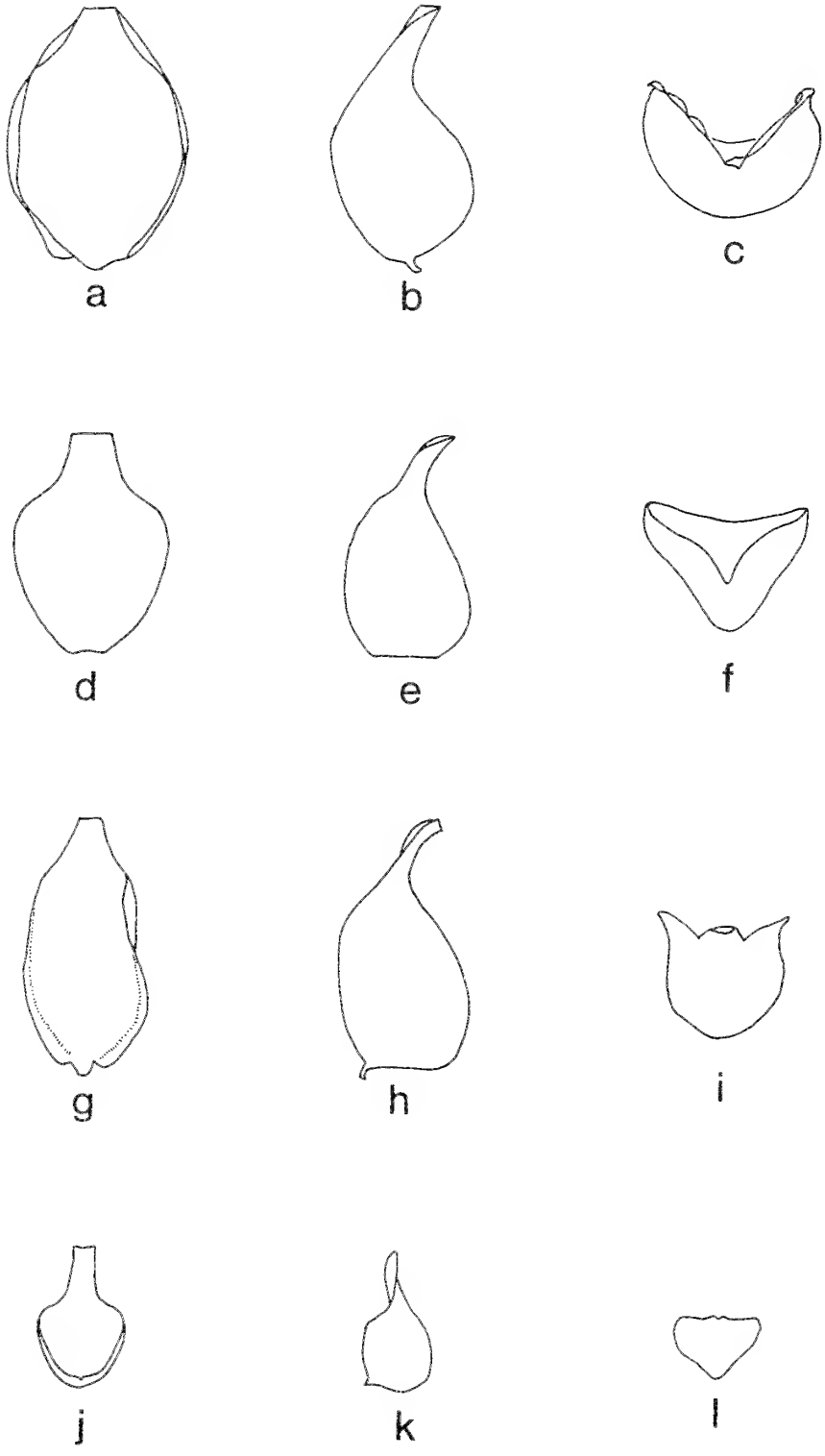


FIGURE 24.—Medial petals of four species of *Aneilema* section *Lamprodithyros: a–c, A. clarkei* Rendle (from *Evans & Maikweki 51*); *d–f, A. lamuense* Faden (from *Faden & Faden 74/1083*); *g–i, A. succulentum* Faden (from *Faden et al. 70/937*); *j–l, A. zebrinum* Chiovenda (from *Faden et al. 74/330*). All are after stamens have been released (where appropriate). (*a,d,g,j*, front views; *b,e,h,k*, lateral views; *c, f,i,l*, apical views.) (Bar = 1 mm.)

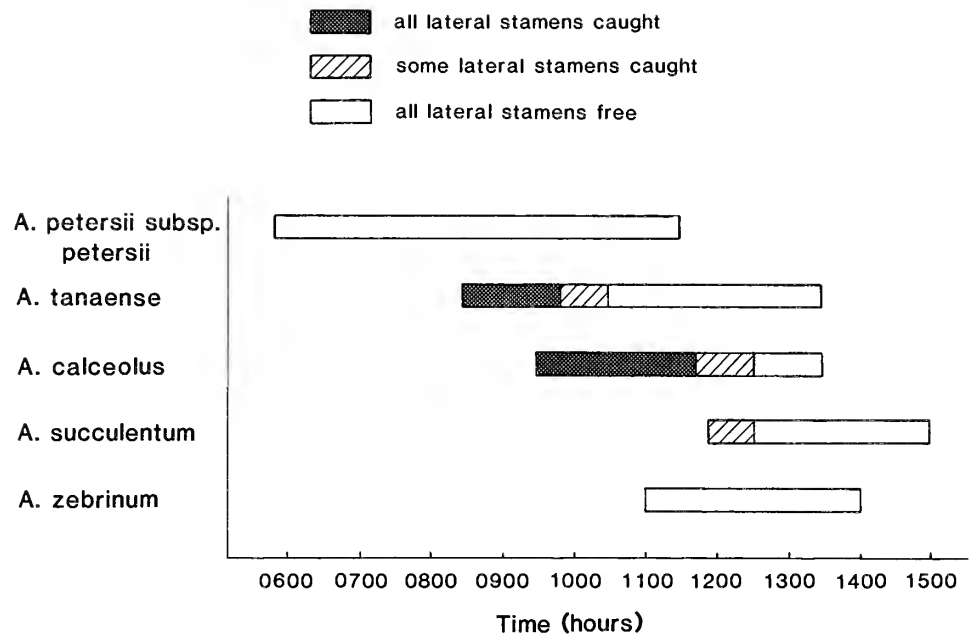


FIGURE 25.—Flowering times and lateral stamen retention in five species of *Aneilema* section *Lamprodithyros* in Kenya. The bars represent the interval between the opening of the first flower and onset of fading.

num, and *A. taylorii* are shown in Figures 17, 47*c,e* and Plates 1*n,p,* 2*b–d,* respectively.

The sterile anthers or antherodes of the staminodes are typically bilobed (Figure 43). In *A. neocaledonicum* (Plate 1*c*), however, they are primitively scarcely lobed, while occasionally in other species they may be unlobed or hardly lobed through reduction. The lobes show much variation in shape according to the species. They may be sessile or stalked, the length of the stalk and angle of its attachment to the filament being characteristic in some taxa. The antherodes of all staminodes are generally yellow except in *A. acuminatum* (Plate 1*a,b*), in which they may be white or violet; in *A. rendlei* and *A. taylorii* (Plate 1*m,o*), in which the lobes of at least the medial staminode are maroon-spotted adaxially; and in *A. lamuense* (Plate 4*b,c*), in which the lobes have pinkish purple bases. The staminode lobes vary further in being either thin and flat or thick and tumid. Their surface is generally more or less smooth, but in *A. welwitschii,* it is verrucose. The connective is sometimes slightly elongate between the staminode lobes, appearing as an extension of the filament to which the lobes are seemingly subterminally attached.

All characters of the staminodes are useful taxonomically. The most important are relative degree of development of medial and lateral staminodes, particularly of their antherodes, presence or absence of a strong curvature in the filaments, and shape and size of the antherode lobes. Staminode characters must be used with caution because, although relatively constant in some taxa, e.g., *A. rendlei* and *A. petersii,* they are variable in others, e.g., *A. hockii* and *A. indehiscens* subsp. *lilacinum.*

Although the staminodes completely lack pollen, their function appears to be the attraction of pollinators. The usual yellow color of the antherodes may make them appear polleniferous to some insects. The staminodes may further attract pollinators by producing a scent in some taxa. Several flowers of *A. somaliense* were dissected into separate floral organs: sepals, petals, staminodes, stamens, and gynoecium. The staminodes appeared to be one source of the scent produced by these flowers, but the results were inconclusive. The possibility that the antherode lobes in *Aneilema* may be sources of liquid for pollinators, as has been suggested for *Commelina* staminodes by Faegri and Pijl (1971:71), has not been ruled out, but field observations of numerous flower visitors have thus far failed to support this hypothesis.

Stamens: In all *Aneilema* species—except *A. neocaledonicum* (Plate 1*c*), in which the three stamens are more or less equal—the lateral stamens always have longer filaments and further differ in filament curvature and anther form from the medial stamen. One aspect of lateral filament curvature that varies among species is the relationship of the filaments to each other, i.e., whether they are divergent, parallel, or convergent. This can be determined most satisfactorily from a top view of the flower. The filaments may be closely parallel for their entire length, as in *A. aequinoctiale* (Plate 1*i*), but more commonly, they are divergent for at least part of their length. In some species different parts of the filament regularly have different degrees of convergence or divergence (Figures 26*d,* 28*a*). The lateral filaments cross in *A. petersii* (Figure 26*b;* Plate 2*m–p*), the only species in which this character is typical. Top views of

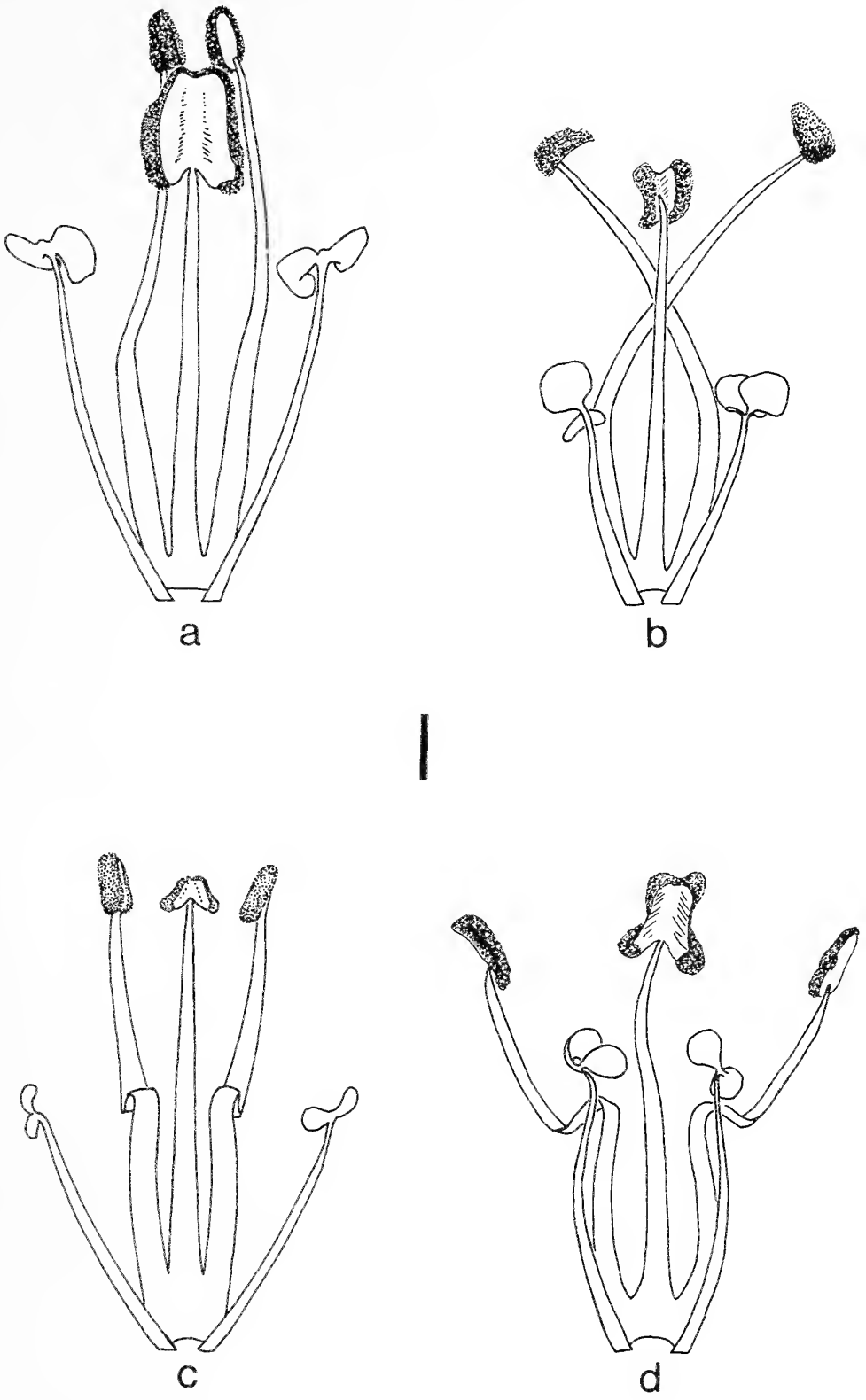


FIGURE 26.—Top views of the androecia of four species of *Aneilema* section *Lamprodithyros*, medial staminode omitted, gynoecium removed: *a*, *A. indehiscens* Faden subsp. *indehiscens* (from *Faden & Faden 72/72*); *b*, *A. petersii* (Hasskarl) C.B. Clarke subsp. *petersii* (from *Andrews s.n.*); *c*, *A. forskalii* Kunth (from *Gilbert & Thulin 969*); *d*, *A. recurvatum* Faden (from *Faden 69/1300*). (Bar = 1 mm.)

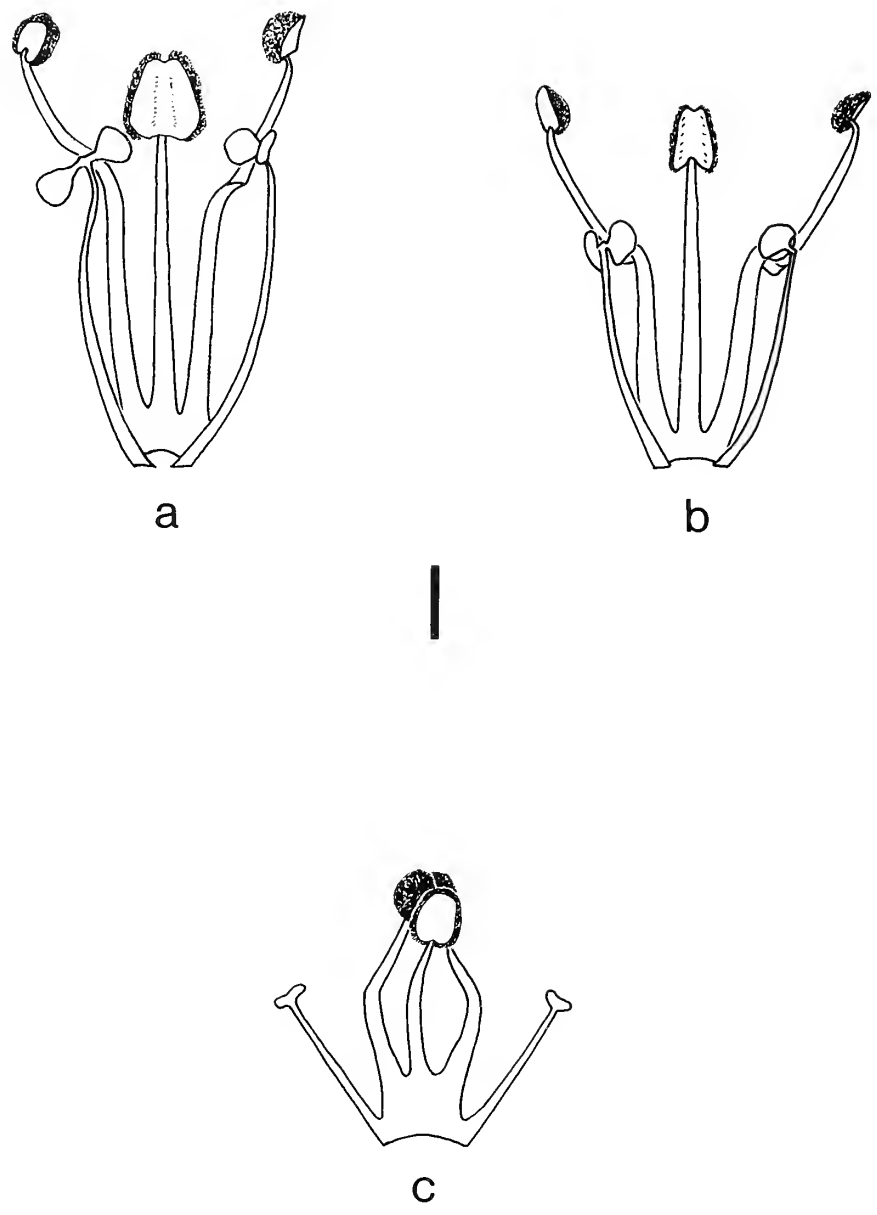


FIGURE 27.—Top views of the androecia of three species of *Aneilema* section *Lamprodithyros*, medial staminode absent or omitted, gynoecium removed: *a*, *A. tanaense* Faden (from *Gillett 19973*); *b*, *A. calceolus* Brenan (from *Faden & Faden 74/1069*); *c*, *A. zebrinum* Chiovenda (from *Faden & Faden 74/482*). (Bar = 1 mm.)

the filaments of 12 species of section *Lamprodithyros* are shown in Figures 26–28, 50*g*, 51*g*.

The aspect of lateral stamen filament curvature that is most important taxonomically is the shape of the filament in lateral view. Four basic types are recognizable: straight, undulate, S-shaped or sigmoid, and J-shaped (Figure 29). The U-shaped curvature mentioned in section *Rendlei*, e.g., Plate 1*p*, is considered a variant of the J-shape, having been derived by reduction of the longer arm. Variation in the angle at which the filaments are held relative to the horizontal can result in the final position of the anthers being quite different in relation to other floral parts, even between species with the same basic curvature type (Figures 29*b–d,f,g*).

The four main curvature types have been useful in defining the sections in *Aneilema*. The lateral stamen filaments are straight or nearly so in section *Aneilema* (Plate 1*a–c*), straight or undulate in section *Amelina* (Plate 1*d-k*), sigmoid in sections *Somaliensia, Lamprodithyros, Brevibarbata,* and *Pedunculosa* (Plates 2*e–p*, 3, 4), and principally J- or U-shaped in section *Rendlei* (Plates 1*m–p*, 2*a–d*). The curvature of the filaments in bud is indicative of that found in the flower (Figure 30). Thus the stamen curvature of species known only from dried

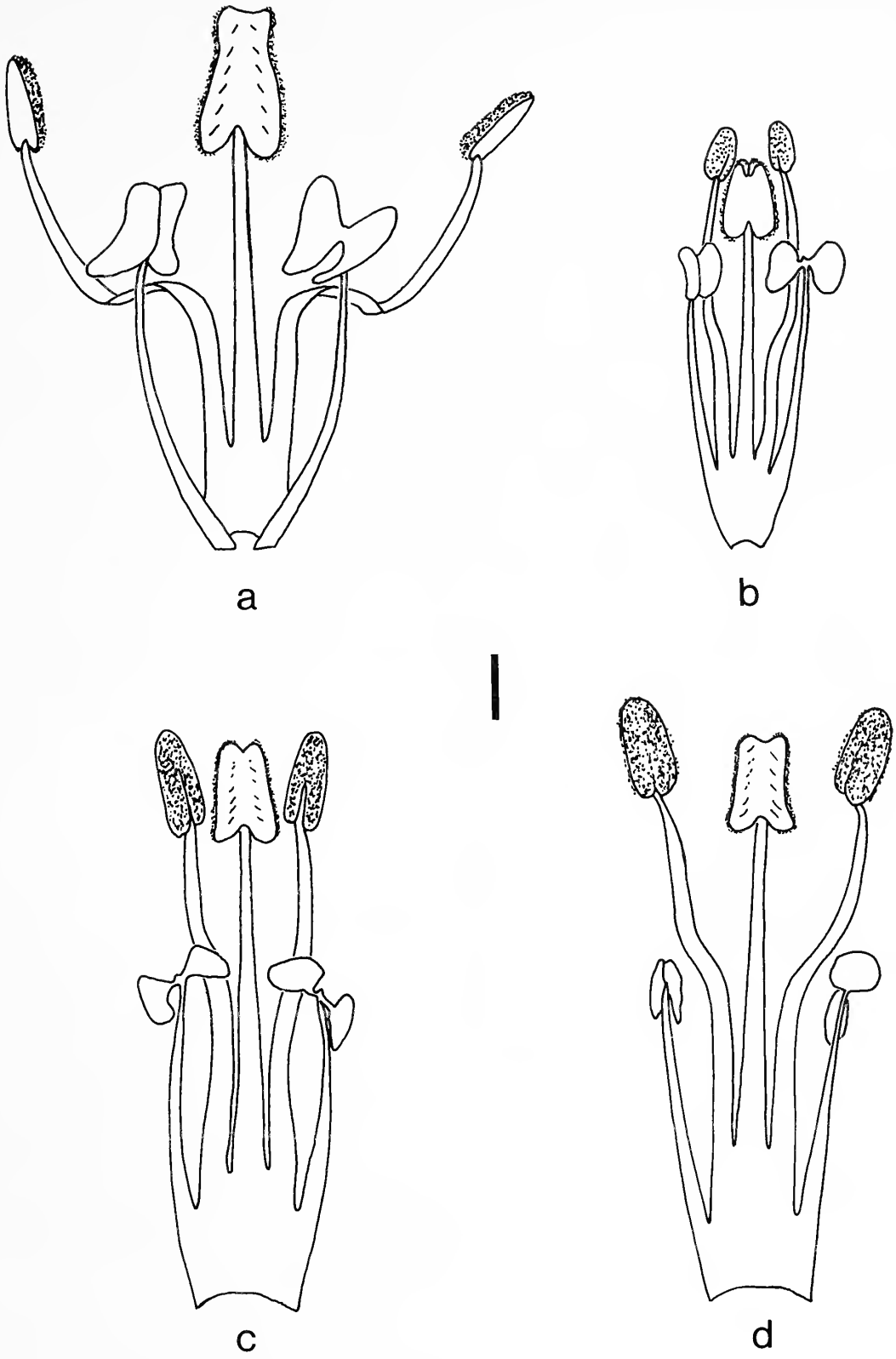


FIGURE 28.—Top views of the androecia of three species of *Aneilema* section *Lamprodithryos*, medial staminode omitted, gynoecium, when present, removed: *a*, *A. clarkei* Rendle (from *Faden & Faden 74/1215*); *b*, *A. succulentum* Faden (from *Faden & Faden 74/1152*); *c,d*, *A. lamuense* Faden: *c*, perfect flower; *d*, staminate flower (from *Faden & Faden 74/1083*). (Bar = 1 mm.)

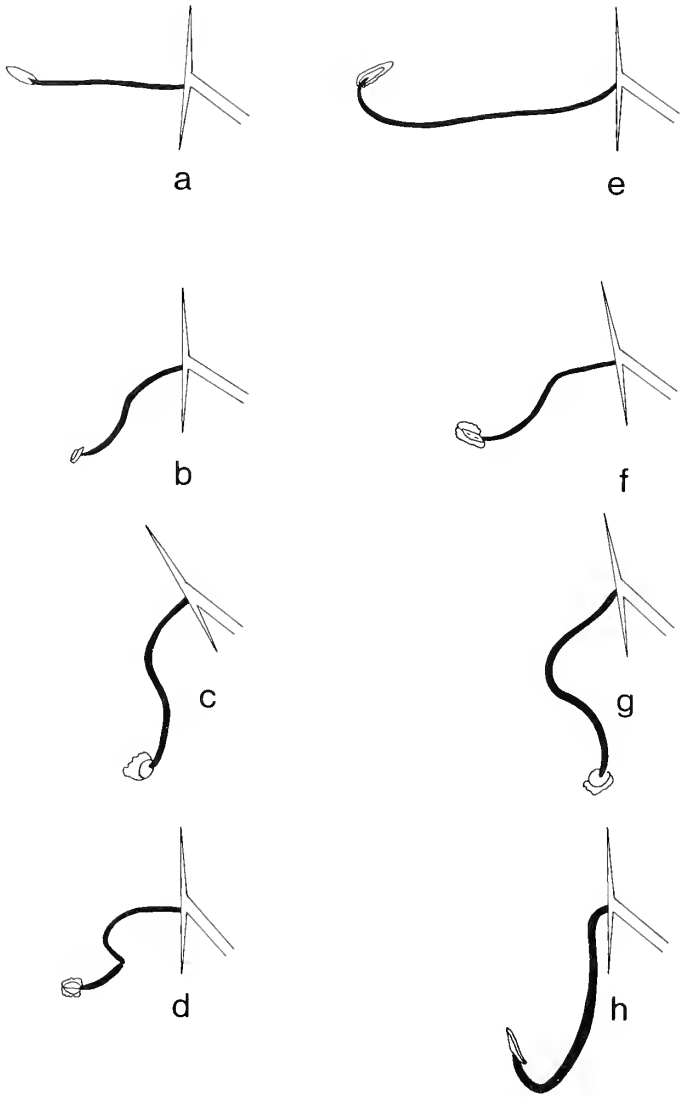


FIGURE 29.—Lateral stamen filament curvature types in *Aneilema: a*, straight; *b-d,f,g*, S-shaped or sigmoid; *e*, undulate; *h*, J-shaped. (Not to scale.)

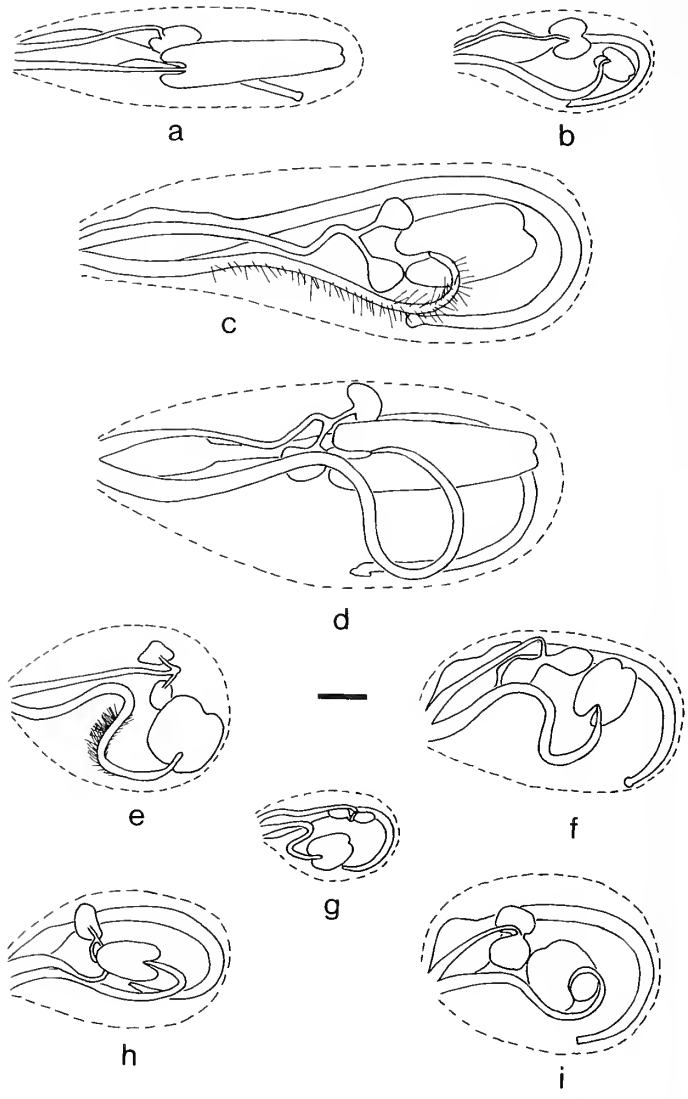


FIGURE 30.—Lateral stamen and lateral staminode filament curvatures in buds of *Aneilema* species: *a, A. neocaledonicum* Schlechter (from *Bierhorst in Kew Accession No. 000-69.12046*); *b, A. acuminatum* R. Brown (from *Hind 683*); *c, A. aequinoctiale* (P. de Beauvois) G. Don (from *Faden et al. 71/922*); *d, A. hockii* De Wildeman (from *Faden et al. 72/234*); *e, A. welwitschii* C.B. Clarke, bud of staminate flower (from *Faden et al. 74/177*); *f, A. recurvatum* Faden (from *Faden et al. 69/1066*); *g, A. somaliense* C.B. Clarke (from *Faden & Faden 74/923*); *h, A. rendlei* C.B. Clarke (from *Kabuye & Evans 163*); *i, A. petersii* (Hasskarl) C.B. Clarke subsp. *petersii* (from *Faden & Faden 74/291*). All buds are from cultivated plants. In flower, *a-c* have lateral stamen filaments straight; *d*, undulate; *e-g,i*, S-shaped or sigmoid; *h*, J-shaped. (Bar = 1 mm.)

specimens can often be deduced through careful dissection of mature buds.

The lateral stamen filaments are either glabrous or variously bearded. The presence or absence of hairs on the filaments is a specific character in *Aneilema*. It does not vary within a species, unlike the apparent situation in some *Murdannia* taxa (see Clarke, 1881a:207, under *Aneilema spiratum* = *Murdannia spirata*). Filament pubescence is also significant at the sectional level: sections *Aneilema, Rendlei, Somaliensia,* and *Lamprodithyros* are characterized by glabrous filaments, and sections *Brevibarbata* and *Pedunculosa* by bearded filaments. Only section *Amelina* includes some species with glabrous and others with bearded filaments. Considerable variation in the types of hairs and in their distribution on the lateral stamen filaments is present in the genus as a whole, but on closer inspection, all of the unusual types and distributions occur solely in section *Amelina* and are usually restricted to single species. The only generalizations that hold for all species are that the hairs are never moniliform and that they are attached predominantly or exclusively to the abaxial surface of the filament. The hairs are generally uniseriate and eglandular, with a rounded terminal cell, but branched hairs (*A. nyasense*), glandular hairs (*A. gillettii*), and hook-hairs (*A. aequinoctiale*)

also occur (Figure 41; Table 4). Typically the hairs are present only distal to the middle of the filament, but in *A. nyasense* and *A. aequinoctiale* (Plate 1*i,j*) they are distributed along most of its length, and in *A. gillettii* (Plate 1*f*) they are found only below the middle. The hairs vary in length from about 40 to 1000 µm. They may be very short, whitish and easily overlooked, e.g., in *A. pomeridianum* (Plate 4*k*), or long, brightly colored, and very conspicuous, as in most species of section *Pedunculosa* (Plate 4*m–p*).

The lateral filaments may be terete or strongly flattened dorsiventrally and ribbon-like. In section *Pedunculosa*, they are broadened in the region to which the hairs are attached. The character of lateral stamen dimorphism is discussed above.

The filament of the medial stamen is much less variable than those of the lateral stamens. It is always glabrous, usually straight or gently arcuate, and often slightly to strongly recurved apically.

Aneilema anthers are four-celled and longitudinally dehiscent (Figure 31). The lateral and medial stamen anthers vary in relative degree of development, shape, size, form of the connective, color, attachment, orientation, and pollen color. The medial anther may be larger or smaller than the lateral anthers. There is a general inverse correlation between medial anther size and the amount of lateral filament pubescence. The species with glabrous filaments always have the medial anther larger than the lateral anthers. Those with short, inconspicuous hairs on the filaments usually have the three anthers subequal in size, although the medial differs in shape. The species with densely bearded filaments generally have the medial anther distinctly smaller than the laterals. *Aneilema nyasense* (Plate 1*j*) is an exception, for its lateral filaments are minutely bearded, but its medial anther is reduced. *Aneilema gillettii* (Plate 1*e,f*) is also unusual in having finely bearded filaments and an enlarged medial anther.

The lateral anthers, except in *A. biflorum*, have narrow connectives (Figure 31*c,d*). In contrast, the medial anther has a broad connective, with the exception of *A. neocaledonicum* (Figure 31*a,b,e,f*). The medial anther connective may be shorter than the anther sacs, the whole anther thereby bowtie- or dumbbell-shaped, e.g., *A. beniniense*, *A. nicholsonii*, and *A. welwitschii*, or more or less equal in length to the anther sacs. In the latter case the anther may be shield-shaped, e.g., *A. ephemerum* and *A. johnstonii*, saddle-shaped, e.g., *A. hockii* and *A. petersii* (Plates 1*h,l*, 2*n,p*), or convex-ellipsoid, e.g., *A. rendlei* and *A. taylorii* (Plate 1*m–p*). The connectives of the larger medial anthers are commonly strikingly spotted or transversely striped with maroon (Plate 1*m–p*). The anthers of *A. neocaledonicum* and *A. biflorum* are basifixed. More generally, however, the anthers are slightly dorsifixed. The enlarged medial anthers are usually versatile; the lateral anthers are not distinctly versatile.

The thecae of all three anthers in *A. neocaledonicum* and *A. biflorum* are situated on opposite ends of the connective (Figure 31*a,b*). The anther dehiscence is latrorse. In all other *Aneilema* species the anther sacs in at least the lateral anthers are both located on one side of the connective or, in the case of the large medial anther, usually face in more or less the same direction due to the outgrowth of the connective (Figure 31*c–f*). The varied orientation of the anthers, erect, horizontal, or pendent, usually results in an introrse dehiscence. However, the lateral anthers of *A. petersii* (Plate 2*n,p*) and of one population of *A. hockii* and occasionally the medial anther of *A. dregeanum* subsp. *dregeanum* have a more or less extrorse dehiscence.

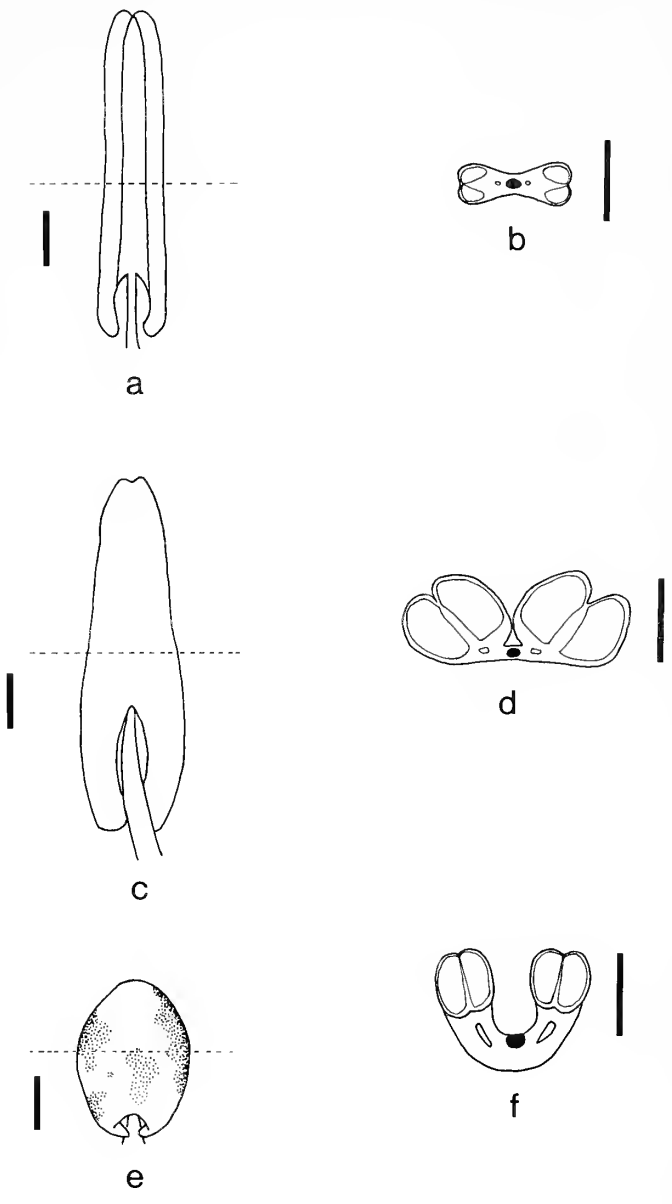


FIGURE 31.—*Aneilema* anthers. *A. neocaledonicum* Schlechter (*a,b*): *a*, anther; *b*, transverse section of *a* (from *Bierhorst in Kew Accession No. 000-69.12046*). *A. hockii* De Wildeman (*c,d*): *c*, lateral anther; *d*, transverse section of *c* (from *Faden et al. 72/234*). *A. taylorii* C.B. Clarke (*e,f*): *e*, medial anther; *f*, transverse section of *e* (from *Faden & Faden 74/371*). The broken lines indicate the planes of the sections. (Bars = 0.5 mm.)

The medial stamen has been considered staminodial in five West African *Aneilema* species (*A. beniniense, A. lanceolatum, A. pomeridianum, A. setiferum,* and *A. umbrosum*) by Morton (1966). West African populations of *A. beniniense, A. umbrosum,* and *A. lanceolatum* subsp. *lanceolatum* have been checked and the medial anthers found to produce viable pollen (Table 1). In view of these results and of the observation that even more reduced medial anthers of other *Aneilema* species usually produce some pollen, Morton's description of the medial anthers of the other two West African species as staminodial requires confirmation.

The pollen grains in *Aneilema* vary in color from white to yellow or orange. Commonly the pollen of the medial anther differs in hue from that of the lateral anthers. This color difference is sometimes taxonomically useful. For example, in *A. calceolus* (Plate 3*n,o*) the medial anther has yellow pollen and the lateral anthers white pollen, while in the closely related *A. tanaense* (Plate 3*l*), all three anthers have yellow pollen. Similarly, *A. clarkei* has yellow and white pollen in the medial and lateral anthers, respectively. Its close relative *A. lamuense* has white pollen in all anthers, the only *Aneilema* species noted with this character. In *A. taylorii* the pollen color differentiation is less conspicuous than in *A. calceolus* or *A. clarkei:* the lateral anther pollen is usually orange-yellow and the medial anther pollen yellow when the flower first opens. During the course of flowering, the pollen grains of the medial anther turn white, and so when the flower begins to fade, usually only white pollen is present in this anther. No such color change occurs in the lateral anther pollen; hence pollen color differentiation increases during the flowering period.

A further difference occurs in *A. hockii* pollen. The medial anther pollen differs not only in color but also in stainability with cotton blue, an indicator of viability. All of its pollen grains stain weakly and show shriveled contents; they are apparently inviable. In contrast, 96%–98% of the lateral anther pollen grains stain strongly and appear viable (Figure 15; Table 1). In one population both types of pollen grains were equal in size in the three flowers checked. In a single flower from another population, the medial anther pollen grains were distinctly longer than those of the lateral anthers. Such differences in pollen stainability and size have previously been reported in the Commelinaceae only in *Tripogandra* (Lee, 1961; Handlos, 1970, 1975; Mattsson, 1976; Poole and Hunt, 1980) and *Palisota* (Faden, 1983c, 1988). No variation in pollen size or staining was found in the anthers of five other *Aneilema* species (Table 1).

Aneilema pollen grains are monosulcate and ellipsoid to bean-shaped or sometimes irregularly spherical. Scanning electron micrographs (Figures 32, 33) show that the exine is spinulose or spinulose-verrucose and punctitectate. The spinules or warts are blunt and randomly arranged. Lengths of 32, 33, 53, and 59 µm have been reported for the pollen grains of four unnamed species by Erdtman (1966) and of 63–91 (mean 76.9) µm for *A. aequinoctiale* by Zinderen Bakker (1953). Poole and Hunt (1980) report mean diameters for six species ranging from 32.1 µm to 68.5 µm. The lengths of five species measured in the present study ranged from 30.5 µm to 47.6 µm (Table 2). The results of Poole and Hunt (1980) suggest that the following pollen characters may be useful taxonomically at the species level: dimensions of the pollen grain; length of the spinules and distance between them; and thickness of the wall. Populations of additional species need to be investigated before the general usefulness of pollen characters in *Aneilema* can be confirmed.

All stamen characters are useful taxonomically. The most important are the presence or absence of filament fusion, dimorphism, and pubescence; type of filament curvature; relative size of lateral and medial anthers; form of the medial anther; and pollen color.

Staminode and stamen filament lengths are measured curvilinearly and include the length of the fused basal portion, when present. Antherode and anther measurements are linear. Antherode lobe length is measured at right angles to the staminode filament, or, when the lobes are stipitate, then parallel to the stalk. Lobe length does not include the stalk. Lobe width is measured at right angles to the length.

GYNOECIUM.—The gynoecium consists of a basically trilocular ovary and a simple, terminal style and stigma. The ovary may be sessile or stipitate, but the distinction between these conditions is seldom clean-cut. Three longitudinal lines

TABLE 1.—Pollen viability in *Aneilema* species (the first 100 pollen grains encountered were tallied; * = well-formed pollen grains that stained darkly with cotton blue were considered viable).

Taxon	Collection	Ploidy	Number of buds	Lateral anther pollen % viable*	Medial anther pollen % viable*
Aneilema hockii	*Faden et al. 72/234*	2*x*	3	96–98	0
A. hockii	*Faden & Evans 71/502*	2*x*	1	97	0
A. rendlei	*Kabuye & Evans 163*	2*x*	2	99	99–100
A. clarkei	*Faden et al. 71/633*	6*x*	2	98	99
A. lanceolatum subsp. *lanceolatum*	*Lock 84/93*	2*x*	3	87–94	86–91
A. beniniense subsp. *beniniense*	*Faden et al. 74/71*	4*x*	2	99–100	99–100
A. umbrosum subsp. *umbrosum*	*Faden et al. 74/2*	4*x*	2	5–26	29–50

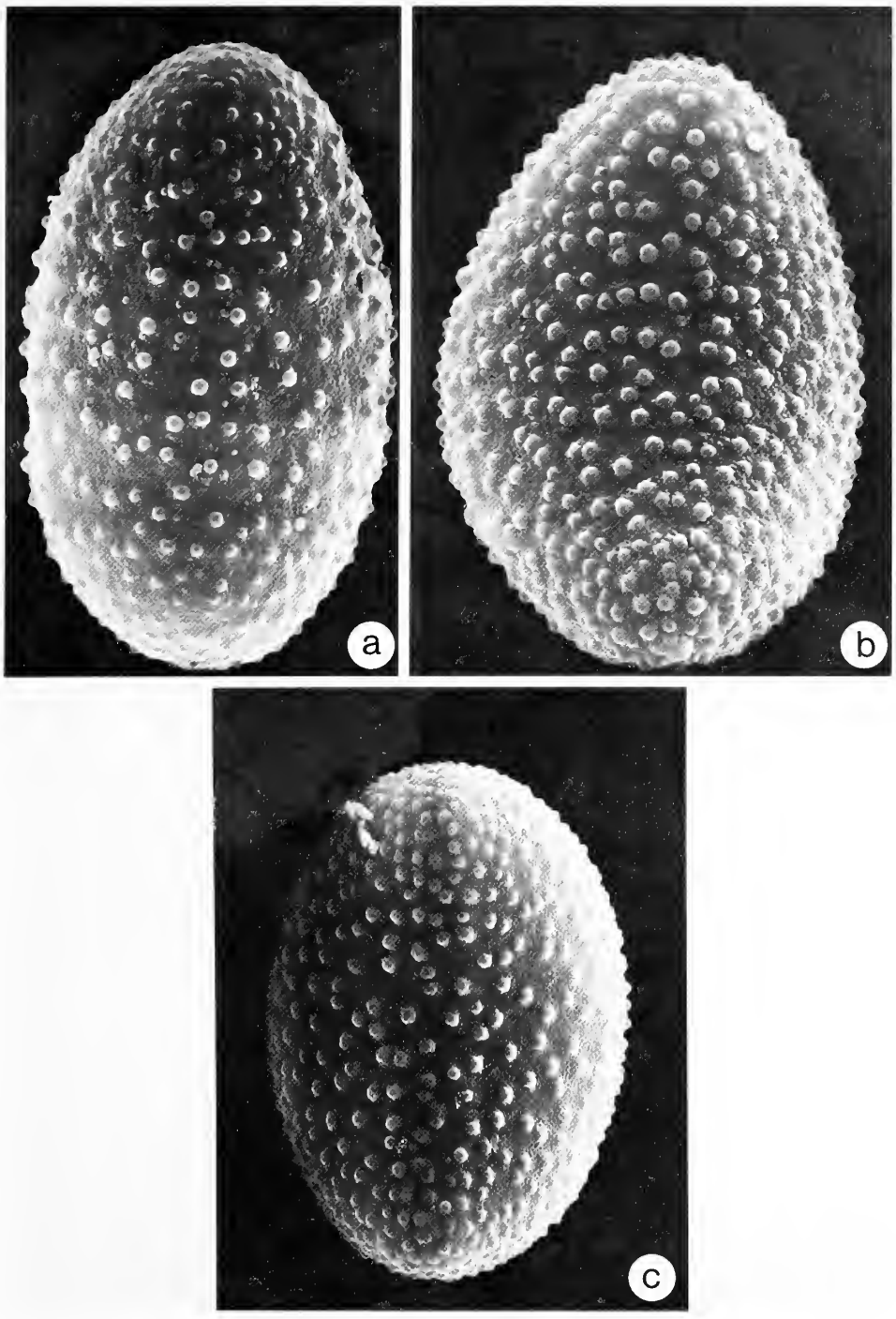


FIGURE 32.—Scanning electron micrographs of acetolyzed *Aneilema* pollen grains (polar view): *a, A. petersii* (Hasskarl) C.B. Clarke subsp. *pallidiflorum* Faden, ×2945 (from *Faden & Faden 74/237*); *b, A. somaliense* C.B. Clarke, ×3400 (from *Faden & Faden 74/923*); *c, A. beniniense* (P. de Beauvois) Kunth, ×2890 (from *Faden et al. 74/71*).

are always visible, a middorsal and two lateral sutures. The latter represent lines of dehiscence in the capsule. In nearly all *Aneilema* species, the middorsal suture is a vestige of a former line of dehiscence. Only in some plants of *A. acuminatum* does dehiscence regularly occur along this suture. The ovary is generally entirely green, but in some species distinctive violet patches, spots, or stripes are present apically.

The ovary may be glabrous or variously puberulous with

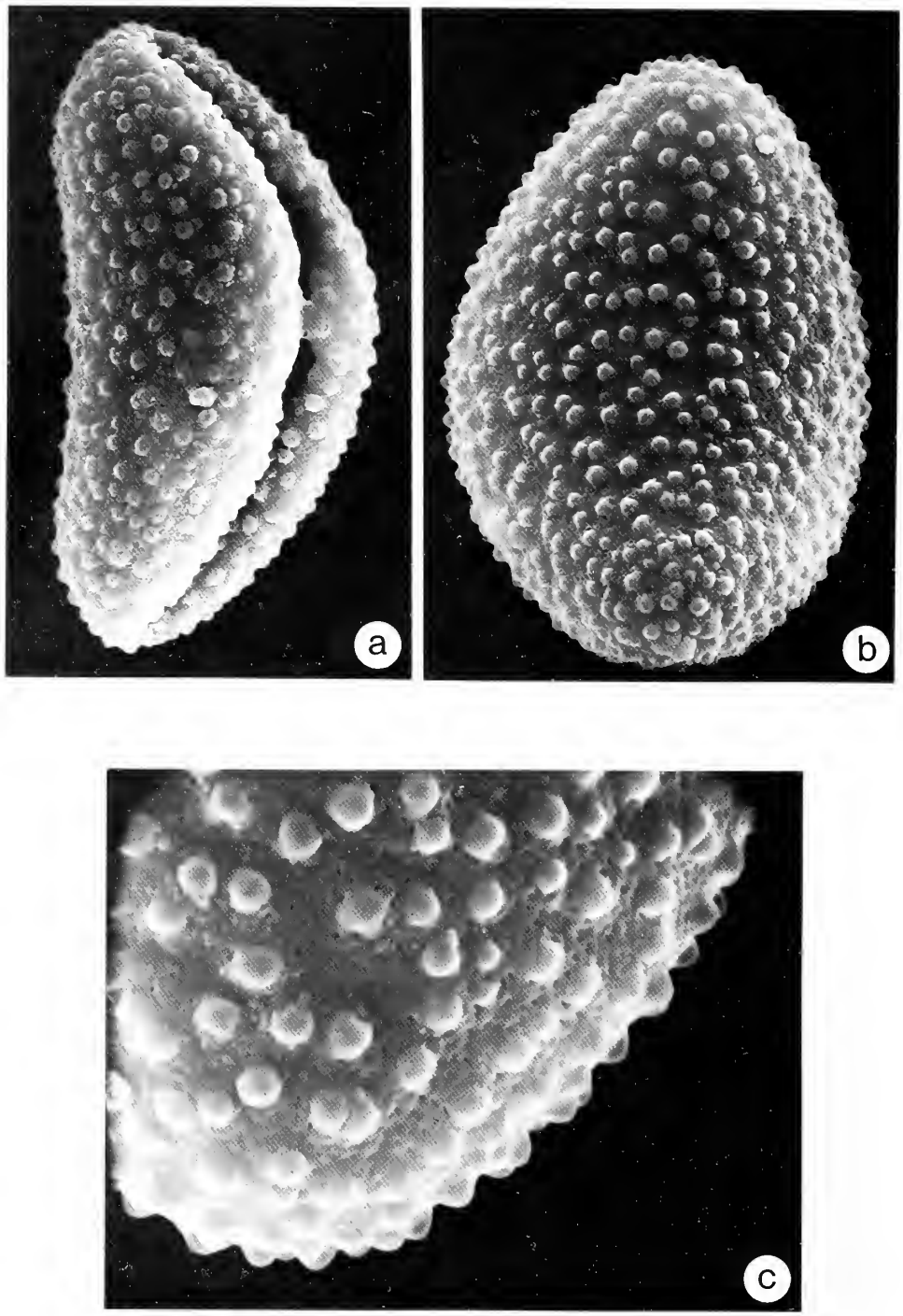


FIGURE 33.—Scanning electron micrographs of pollen grains of *Aneilema somaliense* C.B. Clarke: *a*, equatorial view, longitudinal position, ×3400; *b*, polar view, ×3400; *c*, portion of exine, ×8500. (All from *Faden & Faden 74/923*.)

glandular and occasionally other hair types. The glandular hairs may be appressed microhairs or longer, appressed to patent, uniseriate hairs. The latter may have a globose to ovoid and capitate or a more or less cylindrical, non-capitate terminal cell. Other hair types observed on ovaries are hook-hairs and prickle hairs (Figure 42; Table 5, p. 49). Some sections of the genus are characterized by the distribution and types of hairs present on the ovary. For example, the species of section *Rendlei* have

TABLE 2.—Pollen grain lengths in some *Aneilema* species.

Taxon	Collection	Treatment	Number of pollen grains measured	Mean length (μm)
Aneilema hockii	*Faden et al. 72/234*	cotton blue[1]	15	47.6
A. rendlei	*Kabuye & Evans 163*	cotton blue[1]	15	30.5
A. somaliense	*Faden & Faden 74/923*	acetolyzed[2]	15	32
A. petersii subsp. *pallidiflorum*	*Faden & Faden 74/237*	acetolyzed[2]	15	38.9
A. beniniense subsp. *beniniense*	*Faden et al. 74/71*	cotton blue[1]	15	31.6
A. beniniense subsp. *beniniense*	*Faden et al. 74/71*	acetolyzed[2]	15	32.8

[1]Pollen grains removed from fresh mature buds and mounted in cotton blue, otherwise untreated.
[2]Pollen grains acetolyzed after Erdtman (1966) and mounted in glycerine jelly.

only glandular microhairs, which are found chiefly on the lateral sutures and ventral surface.

In the majority of *Aneilema* species, the dorsal locule is either empty or completely vestigial but identifiable in transverse section. In the remaining species one (rarely up to five) ovule is present in this locule. Species that regularly or occasionally have an ovule in the dorsal locule occur in all sections of the genus and are especially frequent in sections *Aneilema, Somaliensia, Amelina,* and *Lamprodithyros.* The ventral locules each contain one to six uniseriate, campylotropous ovules. The basal ovule in each locule characteristically has its micropylar end directed towards the dorsal surface of the ovary. Successive ovules alternately face ventrally, then dorsally, and so forth. When reduction in ovule number occurs, as in the later flowers of inflorescences in some *A. hockii* populations, it starts from the apical end of the ovary.

The style is always slender. It is typically glabrous except for an occasional hair of the ovarian type on the base in some species. Four basic curvature types occur (in lateral view): straight, arcuate, undulate, and J-shaped (Figure 34). In the first two the style is sometimes recurved near the apex; in the latter two it is always recurved apically. Straight or arcuate styles that are not apically recurved are frequent in autogamous species.

In most species the style lies in the floral midplane or nearly so. In section *Lamprodithyros,* the styles are usually strongly curved laterally out of the floral midplane (Plates 2*n,p,* 3*a,b,d,g,k,l,n,* 4*d*). The distribution of left-handed and right-handed style curvatures within inflorescences has been studied in *A. recurvatum* and *A. tanaense* and found to be random. Either type is just as likely to occur in flowers of either cincinnus rank. The curvature of the stamen filaments is not affected by the style curvature.

The stigma is terminal, usually capitate, and sometimes colored contrastingly to the style, e.g., in *A. acuminatum* (Plate 1*a*). The largest stigmas, e.g., in pistillate flowers of *A. hockii* (Plate 1*l*), may be somewhat triangular in outline. In some species, particularly those of sections *Rendlei* and *Somaliensia,* the stigma is not at all enlarged, and is termed small in the species descriptions. All enlarged stigmas are called capitate.

Owens and Kimmins (1981) surveyed stigma morphology in the Commelinaceae, including several species of *Aneilema.* Both dry and wet stigmas are reported in the genus, but which

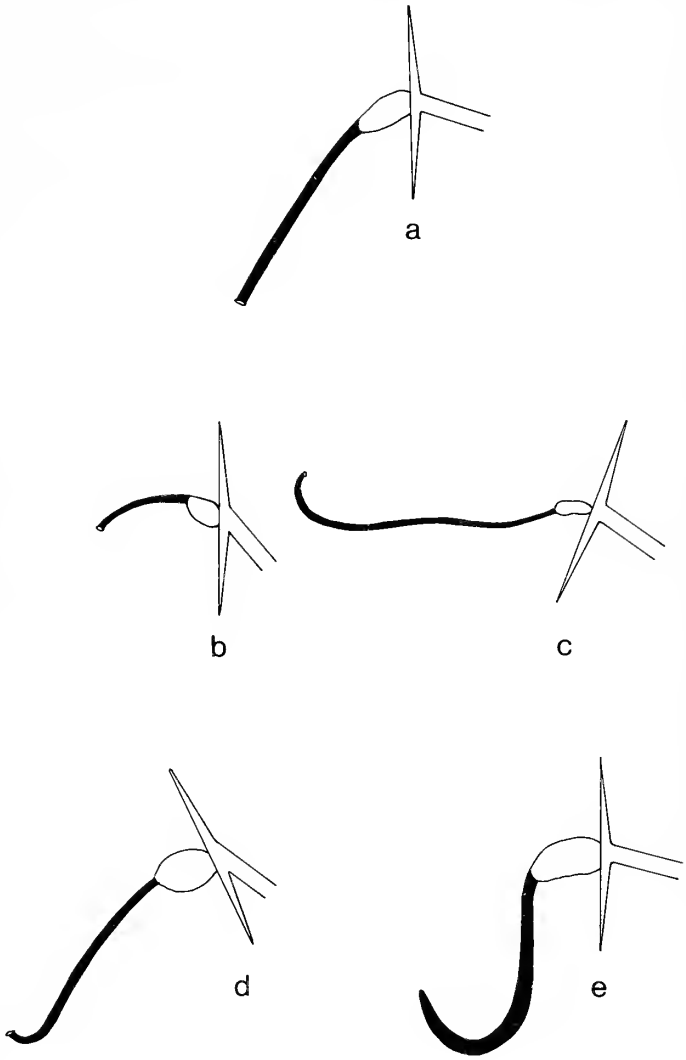


FIGURE 34.—Style curvature types in *Aneilema: a,* straight; *b,* arcuate-decurved; *c,* undulate; *d,* arcuate-decurved, recurved apically; *e,* J-shaped. (Not to scale.)

species have which stigma type is not reeorded. *Aneilema* is reported to be one of only four (out of the 17) genera investigated that lacks raised blisters on the stigma papillae. It also shares with only *Commelina* the character of the papillae covered by a distinetive folded euticle.

In a subsequent paper, Owens and Horsfield (1982) summarize the stigmas of *Aneilema* species as trifid and wet, but in the text they mention that exeeptional stigmas may be eireular in transverse section, and that both dry and wet stigmas were found in plants of *A. aequinoctiale* and *A. hockii*. In one aeeession of the former speeies, exelusively dry stigmas were found.

No list of species was published in either Owens and Kimmins (1981) or Owens and Horsfield (1982), but Hunt (in litt., 23 February 1988) stated that the *Aneilema* speeies used were *A. aequinoctiale* (two aecessions) and *A. hockii*, *A. brenanianum*, and an unnamed speeies (one aeeession eaeh). *Murdannia zeylanica* (C.B. Clarke) Brüekner was also used as an *Aneilema* speeies.

The eharacters of the gynoecium that are most useful taxonomically are ovarian hair types and distribution, dorsal locule development, ovule number in the ventral locules, and style eurvature. Ovary shape is the linear outline viewing the ovary from either the dorsal or ventral surface. Ovary length and width are linear measurements. Length includes the stalk, when present. Style length is curvilinear.

CAPSULES.—*Aneilema* capsules are sessile or stipitate, dry, usually dehiscent, bi- or trilocular, generally bivalved, usually lustrous, and gray to brown or stramineous. As in the case of the ovary, there is no clear distinction between sessile and stipitate capsules. The most plainly stipitate capsules are in the species group of *A. grandibracteolatum*, *A. obbiadense*, and *A. longicapsa* (section *Somaliensia*) and in several speeies of seetion *Lamprodithyros*, e.g., *A. forskalii* and *A. petersii* (Figure 35*a*,*b*).

Aside from *A. zebrinum* and some populations of *A. indehiscens*, in which the capsules are regularly or frequently indehiscent or only partially dehiscent, all species have dehiscent capsules. In the dehiscent capsules the valves may spread only slightly (<90°), e.g., *A. aequinoctiale* and *A. hockii*, or widely (90°–180°), e.g., *A. acuminatum*, *A. johnstonii*, and *A. welwitschii*. In some species the dorsal valve is deciduous (sometimes tardily or only oceasionally so) and serves as a disseminule, carrying with it the dorsal locule seed, whieh is usually developed in these speeies (occasionally laeking through abortion). Deciduous dorsal valves have been noted in *A. sclerocarpum* (seetion *Aneilema*), *A. plagiocapsa* (section *Amelina*), *A. pusillum* and *A. somaliense* (section *Somaliensia*), all species of section *Lamprodithyros* to varying extents, exeept *A. zebrinum*, and *A. pedunculosum* (tardily, section *Pedunculosa*).

The eapsules are regularly bivalved exeept in some specimens of *A. acuminatum*. These plants, sometimes segregated as *A. papuanum*, have trivalved capsules with three equal valves and up to five seeds in the dorsal loeule. The prominent terminal ridge on the dorsal locule of *A. indehiscens* subsp. *indehiscens* is also sometimes partially dehiscent middorsally and the capsules thereby partially trivalved.

Capsule pubescence differs from ovary pubescenee in being less dense due to the increased size of the developing fruit. During the two- to three-week development period of the eapsule, the hairs remain functional. At maturity, when the eapsule turns from green to its ripe color, the thin-walled glandular hairs eollapse. When only glandular mierohairs are present on the ovary (section *Rendlei* species and *A. johnstonii* of seetion *Amelina*), the mature capsules appear glabrous.

Seed number per capsule locule is frequently less than the ovule number due to the abortion of ovules or failure of some of them to set seed. The only species in which regular abortion of particular ovules appears to occur is *A. plagiocapsa*. All four ventral ovules abort, while the strongly laterally compressed dorsal loeule produces a single, large seed (~6 mm long), the largest seed known in the genus.

The shape of the cells of the outer wall of the capsule was first used as a taxonomie eharaeter in *Aneilema* by Brenan (1952), who separated *A. aequinoctiale* from *A. hockii* partly on this eharaeter. Brenan (1961) also used eapsule wall eell shape to distinguish *A. dregeanum* from *A. schlechteri*. Faden (1984) showed that this character could be used to separate three closely related species, *A. schlechteri*, *A. brunneospermum*, and *A. arenicola*.

The cells of the capsule wall in *Aneilema* vary from transversely elongate to isodiametric or rarely longitudinally elongate. Transversely elongate eapsule wall cells are the most eommon type, oeeurring in all speeies of seetions *Aneilema*, *Rendlei*, *Somaliensia*, *Lamprodithyros*, and *Pedunculosa*, most species of section *Brevibarbata*, and in *A. gillettii*, *A. hockii* (Figure 36*a*), *A. johnstonii*, and *A. longirrhizum* of section *Amelina*. The eapsule wall cells are isodiametric in *A. aequinoctiale* (Figure 36*b*), *A. ephemerum*, *A. nyasense*, and *A. plagiocapsa* (seetion *Amelina*) and in *A. mortonii* and *A. paludosum* (section *Brevibarbata*). Only *A. brunneospermum* (section *Brevibarbata*) has longitudinally elongate capsule wall eells (Faden, 1984, fig. 1). Because they frequently vary in shape on different parts of the eapsule, cells from the same part of the capsule must be used when comparing different taxa. For standardization, only the cells of the dorsal valve halfway between the eapsule base and apex and halfway between the lateral and middorsal sutures have been described.

In addition to eell shape, the surfaee of the eapsule wall eells shows interspecifie differences when viewed with the scanning electron microscope. The cells of *A. hockii* capsules (Figure 36*a*) are minutely papillose while those of *A. neocaledonicum* (Figure 36*c*) are smooth.

Many capsule characters appear to be useful taxonomically, the most important being eapsule shape, dimensions, dehiscence, loeule number, apex shape, pubescenee, seed number per locule, and shape and surface features of the capsule wall

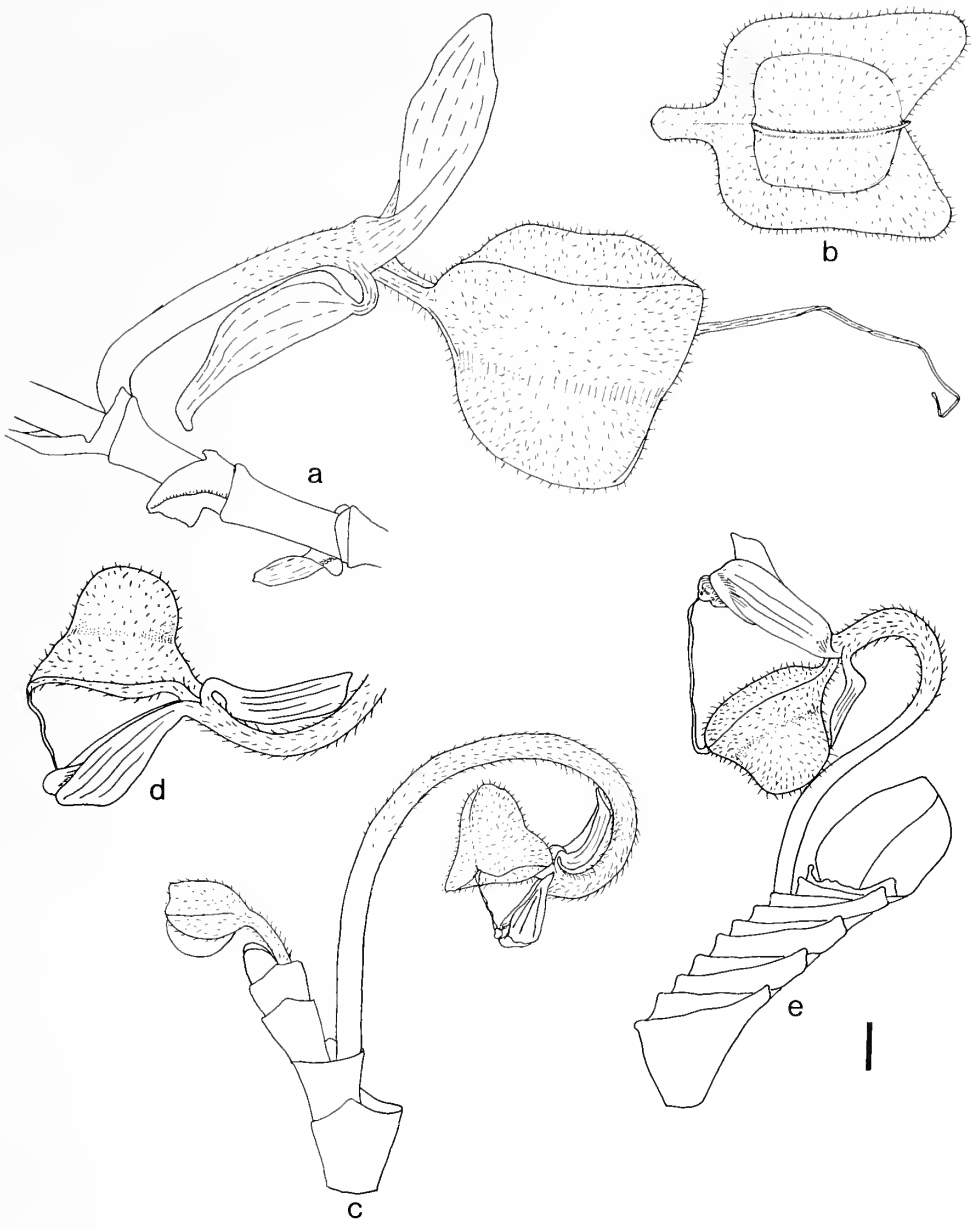


FIGURE 35.—Capsules of *Aneilema* species. *A. petersii* (Hasskarl) C.B. Clarke subsp. *petersii* (*a,b,*): *a,* capsule attached to cincinnus, side view; *b,* dorsal valve, dorsal view (from *Faden & Evans 70/819*). *A. calceolus* Brenan (*c,d*): *c,* capsule attached to cincinnus; *d,* capsule, side view (from *Faden & Faden 74/324*). *A. clarkei* Rendle: *e,* inflorescence with capsule (from *Faden et al. 71/633*). (Bar = 1 mm.)

cells. The capsules are measured in the same manner as the ovaries.

Seeds: *Aneilema* seeds have a linear hilum and prominent, lateral embryotega (Figures 37-39; Plates 5-7). They are usually dorsiventrally compressed, with the ventral surface being planar to slightly concave, and the dorsal surface slightly to strongly convex. The seeds range in length from about 1 to 6 mm, and can reach 3 mm in width and 2 mm in thickness.

Seed shape and size vary according to the species. The shape and size of any particular seed are also determined by its position in the capsule and by the number of other seeds developing in the same locule. The apical end of the apical ventral locule seed is often very different in shape from the basal end of the basal ventral locule seed (Plates 5*a,b,d,f,* 6, 7*f*) and thus these seeds are commonly distinguishable from each other. When more than two seeds are present in each ventral locule, the medial seeds are also distinct in shape from the apical and basal seeds (Plates 5*a,b,d,f,* 6, 7*b,f*). The seeds from

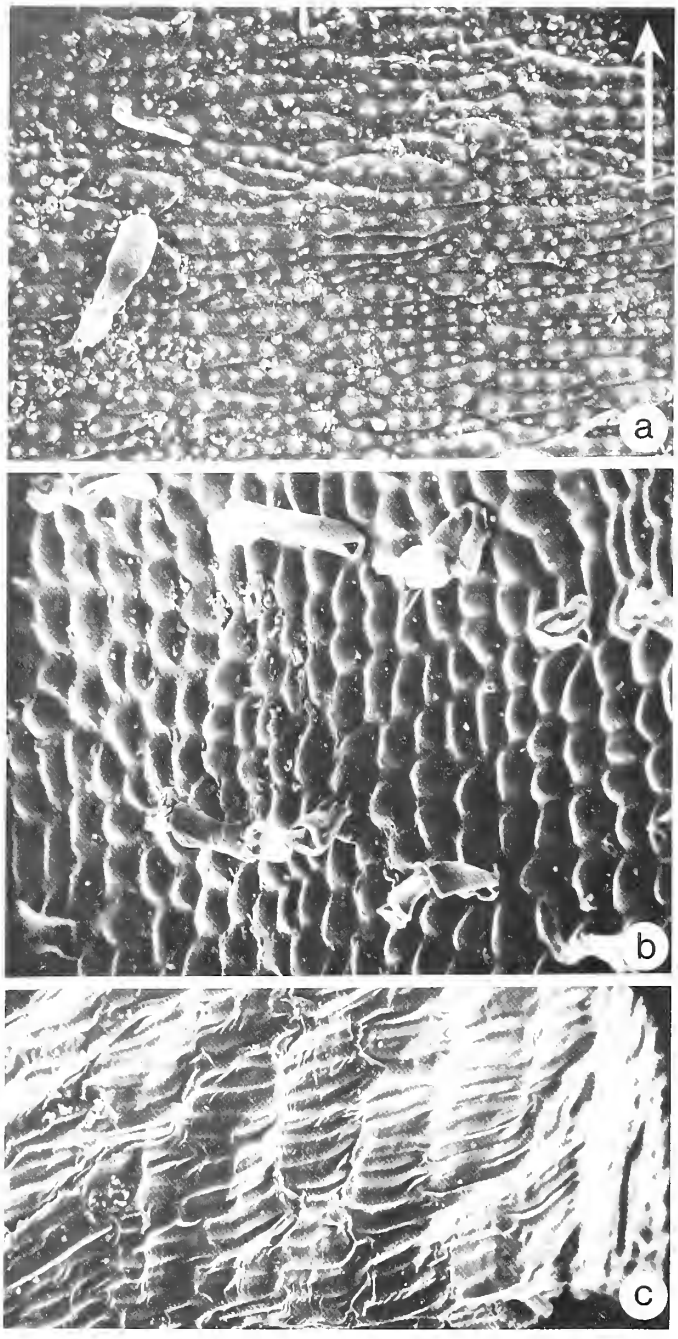


FIGURE 36.—Scanning electron micrographs of *Aneilema* capsule walls: *a*, *A. hockii* De Wildeman, ×~174 (from *Faden & Faden 74/1180*); *b*, *A. aequinoctiale* (P. de Beauvois) G. Don, ×~170 (from *Hall s.n.*); *c*, *A. neocaledonicum* Schlechter, ×~166 (from *Bierhorst in Kew Accession No. 000-69.12064*). The views are of the dorsal valve approximately halfway between the capsule apex and base. The capsule apex is in the direction of the arrow.

one-seeded ventral locules are always longer and somewhat differently shaped from those of two- or more seeded ventral locules of capsules from the same population (Plates 5*a*, 6*e,f*, 7*d*).

In addition to the relatively minor dimorphism or polymorphism among the seeds within the ventral locules, there is sometimes a much greater differentiation between dorsal and ventral locule seeds. Because dorsal locule seeds are almost always solitary and occur only in species having two or more ovules (and generally seeds) in each ventral locule, a difference in size and shape between the seeds of these locules is to be expected. Only such differences in shape and sometimes length between dorsal and ventral locule seeds occur in some species, e.g., *A. indehiscens*, *A. recurvatum*, *A. zebrinum* (Plates 6*b,c*, 7*a*), and *A. grandibracteolatum*.

A more profound dorsal and ventral locule seed dimorphism occurs in other species. These differences may include (in addition to seed shape and length) seed width and thickness, dorsal surface convexity, hilum prominence, embryotega color, testa surface pattern and color, and farinose granule abundance and distribution. The most strongly differentiated dorsal and ventral locule seeds occur in some species of section *Lamprodithyros: A. petersii*, *A. calceolus*, *A. tanaense* (Plate 6*a,f,g*), and *A. forskalii*. Moderately dimorphic dorsal and ventral locule seeds also occur in *A. nicholsonii* (section *Pedunculosa*, Plate 7*b*). It is noteworthy that within section *Lamprodithyros*, the most dimorphic dorsal and ventral locule seeds occur in those species in which the dorsal capsule valves are most regularly deciduous, while the least dimorphic seeds are found in the species with generally persistent capsule valves. The degree of seed dimorphism is probably related to seed dispersal mechanisms in the species of this section.

The hilum usually lies in a longitudinal groove that is open at the apical and basal ends of the seed (Figure 38*c*). Rarely, both ends of the groove are cut off by ridges as in *A. grandibracteolatum*, *A. pusillum*, *A. richardsiae* (Plates 5*c,h*, 7*e*), and *A. longicapsa*. In a few species, mostly in section *Amelina*, the hilum is flush with the ventral surface and not at all in a groove (Figure 37*b;* Plate 15*d,e,j*). The hilum may be confined to the ventral surface or extend onto the apical and/or basal surfaces.

The embryotega is circular to elliptic in outline and has a central prominence. Micropores are visible in scanning electron micrographs (Figures 37*c*, 38*d*). The embryotega is pushed off or to one side by the cotyledon of the germinating seed.

The testa is composed of usually clearly discernible, polygonal cells, each in contact with five to eight cells (Figure 37*d*). Occasionally the cells are less distinct (Figure 39). The testa may be completely smooth, e.g., some populations of *A. hockii* (Figure 37*a;* Plate 5*j*), but more commonly it is variously pitted, grooved, or ribbed. Very regular patterns sometimes occur: alveolate (e.g., some populations of *A. hockii*, Plate 5*e*); reticulate-foveate (e.g., *A. minutiflorum* and *A. umbrosum*, Plate 7*c,g*); sulcate (*A. pusillum*, Plate 5*h*); or ribbed (e.g., *A. paludosum*, Morton, 1966:447, fig. 6). Generally, however, the pits or furrows are irregular, sometimes discrete, sometimes coalescing. The general term used here for such patterns is scrobiculate (e.g., *A. taylorii* and

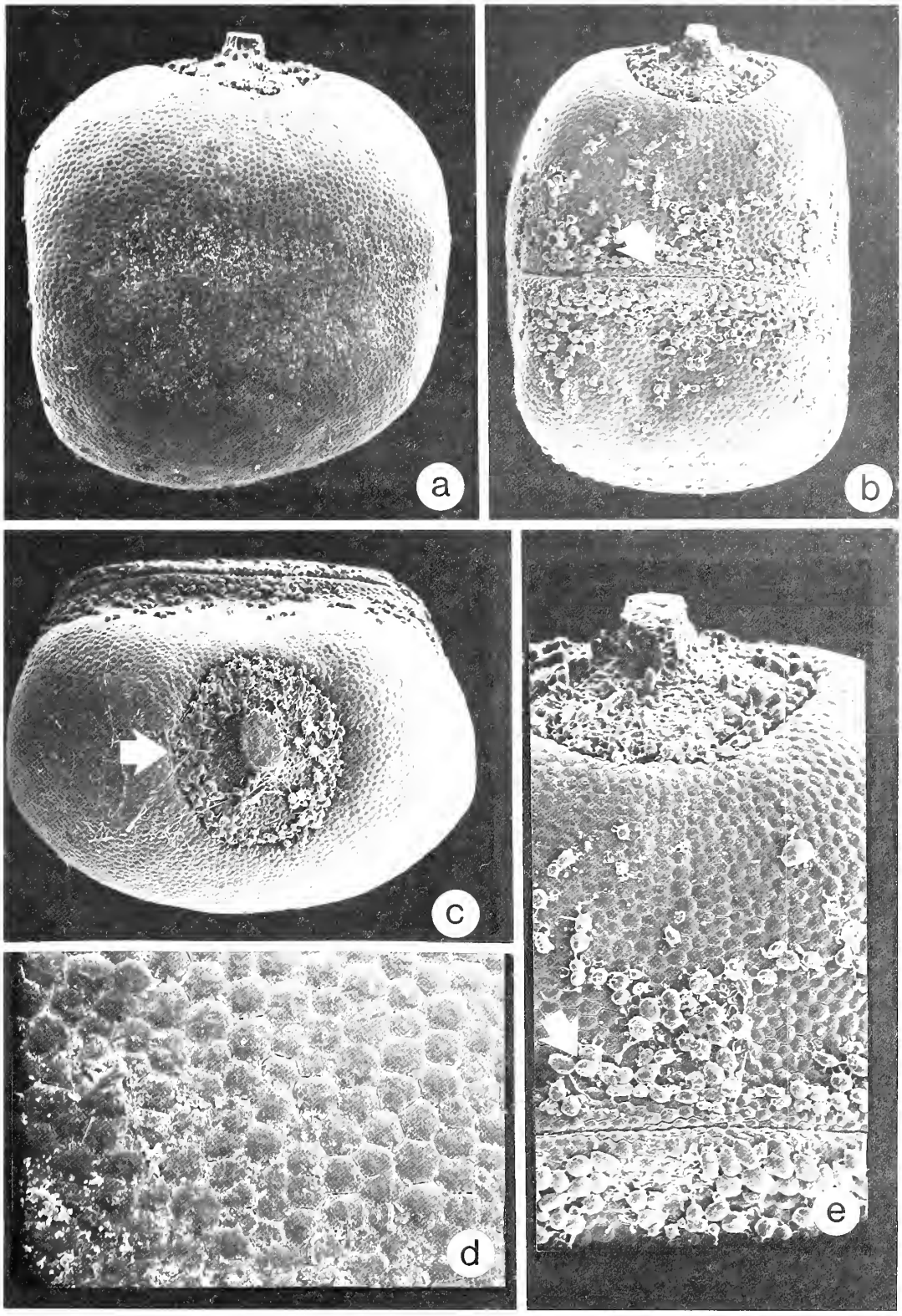


FIGURE 37.—Scanning electron micrographs of seeds of *Aneilema hockii* De Wildeman: *a*, dorsal view, ×~38; *b*, ventral view showing hilum (arrow), ×~38; *c*, lateral view showing embryotega (arrow), ×~38; *d*, dorsal surface cells, ×~197; *e*, ventral view showing farinose granules (arrow), ×~80. All from *Faden & Faden 74/1180*.

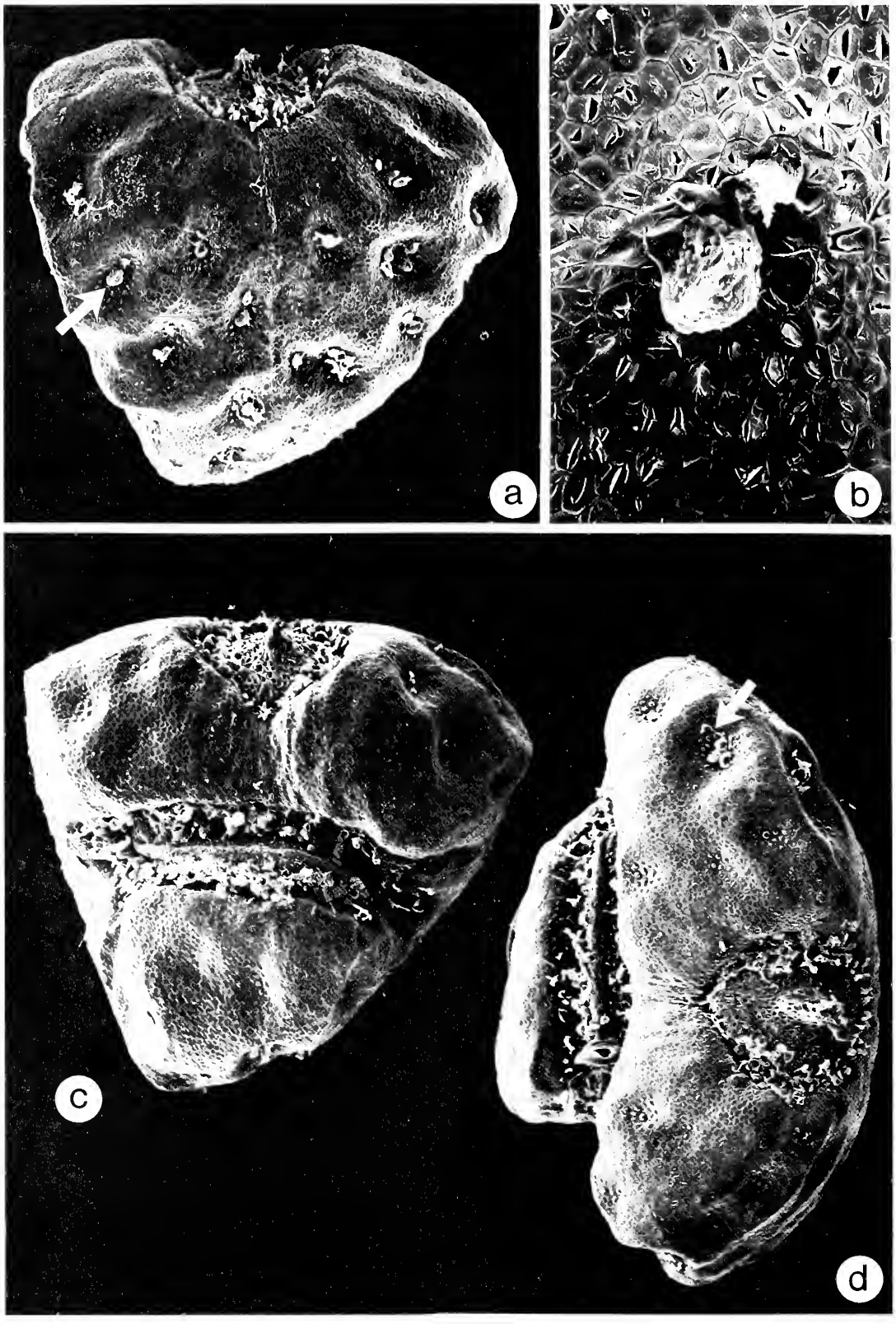


FIGURE 38.—Scanning electron micrographs of seeds of *Aneilema calceolus* Brenan: *a*, dorsal view showing farinose granules (arrow), ×~56; *b*, farinose granules, ×~315; *c*, ventral view, ×~56; *d*, lateral view showing hypha-like filaments (arrow), ×~56. All from *Faden & Faden 74/324*.

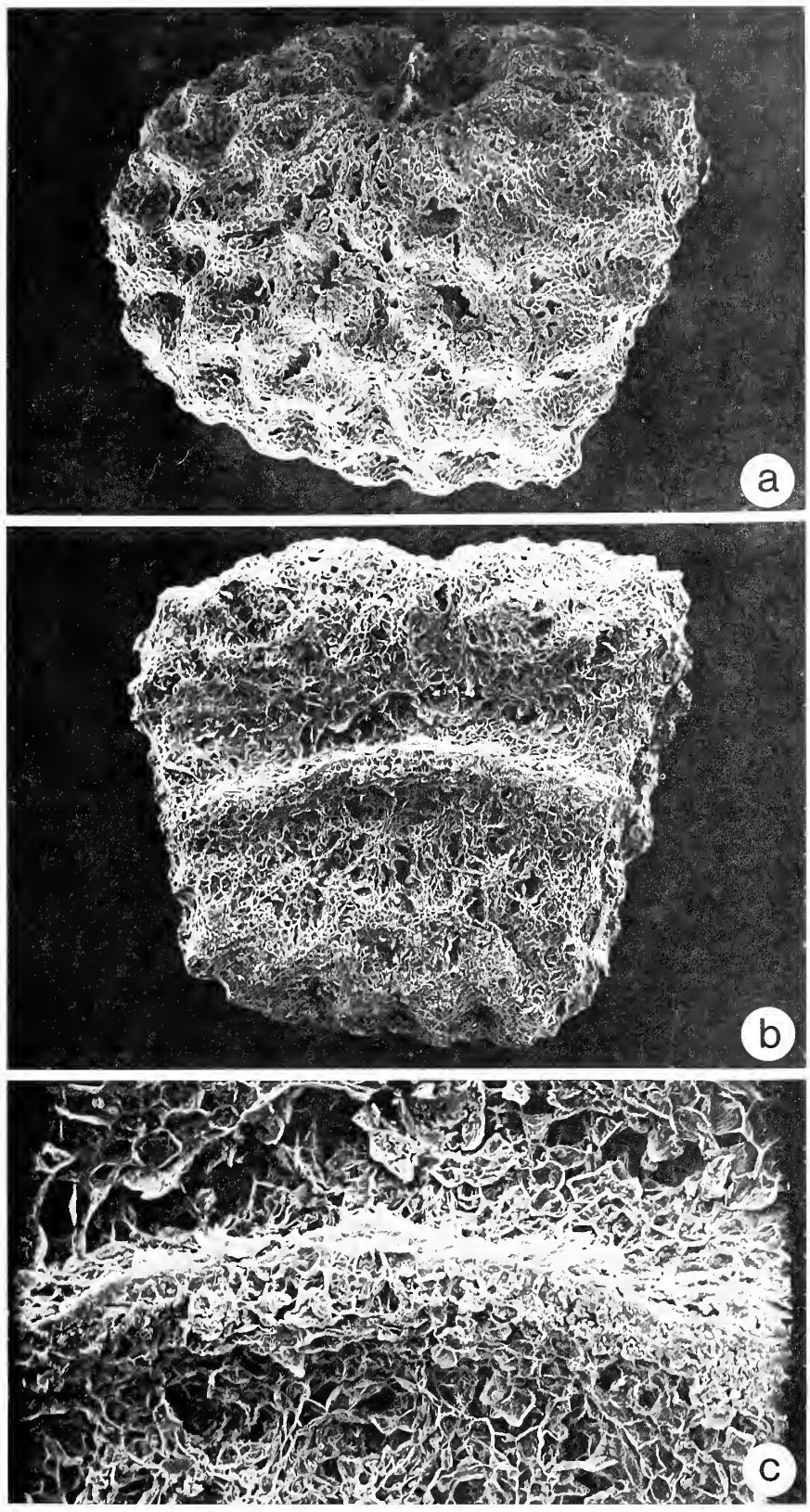


FIGURE 39.—Scanning electron micrographs of seeds of *Aneilema neocaledonicum* Schlechter: *a*, dorsal view, ×~43; *b*, ventral view, ×~43; *c*, region of hilum, ×~115. All from *Bierhorst in Kew Accession No. 000-69.12064*.

ventral locule seeds in *A. calceolus*, Plates 5*a*, 6*f*).

Various particles are often present on the testa. The most common are whitish or light brown (rarely black) granules that I have called farinose granules (Figures 37*e*, 38*a*,*b*). These occur in all sections of the genus except section *Aneilema*. The farinose granules are often confined to the depressions in the testa and to the regions around the hilum and embryotega. Occasionally they may be so abundant that they cover most of the seed surface, as in *A. longirrhizum* (Plate 5*i*). In *A. paludosum* and *A. dregeanum* subsp. *mossambicense* (Faden, 1984), a continuous whitish layer, perhaps derived from fused farinose granules, sometimes covers the entire seed except for the hilum.

Small filaments resembling fungal hyphae sometimes occur among the farinose granules (Figure 38*d*). These have been observed only in species of section *Lamprodithyros*. Their nature has not yet been established.

As has been shown for *Tripogandra* by Handlos (1970, 1975) and for various species of *Floscopa* by Brenan (1952, 1961), seeds are often very useful for specific characters in the Commelinaceae. This has been confirmed for *Aneilema*. The combination of seed shape, dimensions, dimorphism or polymorphism, testa color, and surface pattern is apparently sufficient to distinguish nearly all species. Further scanning electron microscope studies may provide a basis for recognition of all species. Among the three dimensions, seed width is the most useful.

Variation in seed characters between populations of the same species is usually not very great. However, the seeds of the two subspecies of *A. petersii* and *A. dregeanum*, are probably distinguishable from each other. Seeds from West African and East African collections included in *A. dispermum* by Brenan (1952) and Morton (1966) are very different, and it is clear that these geographically isolated populations will have to be separated at the subspecific or specific level when they are studied in detail. Populations of *A. hockii* from the Tana River District of Kenya have very characteristic seeds (Figure 37; Plate 5*j*) that readily separate them from all other populations throughout the extensive range of this species (Plate 5*e*). Further study of *A. hockii* is required in order to determine the taxonomic status of this local variant.

The terminology used for the surfaces of the seed is as follows: ventral, the surface bearing the hilum; dorsal, the surface opposite the ventral; apical and basal, the surfaces facing the apex and base of the capsule, respectively; lateral, the surfaces, one of which bearing the embryotega, directed toward the dorsal and ventral surfaces of the capsule. Seed length is the distance between the apical and basal surfaces; width, the distance between the lateral surfaces; and thickness, the distance between the ventral and dorsal surfaces. Seed shape is the linear outline viewed from the dorsal surface.

Anatomy of *Aneilema*

Introduction to Anatomy

Previous anatomical studies that have included *Aneilema* species are Staudermann (1924)—*A. aequinoctiale*, hairs; Brückner (1926)—*A. beniniense*, all vegetative parts; Rohweder (1963)—*A. beniniense*, stems and flowers; Tomlinson (1966, 1969)—*A. acuminatum*, *A. aequinoctiale*, *A. beniniense*, *A. hockii*, *A. lanceolatum* (including *A. subnudum*), *A. setiferum*, *A. umbrosum*, and *A. zebrinum* (as *Ballya zebrina*), all vegetative parts; Rohweder (1969)—*A. aequinoctiale* and *A. beniniense*, ovaries and seeds; and Walker (1974)—*A. beniniense*, epidermis. This study is of limited scope, intending to survey the variability of certain anatomical characters within *Aneilema* and to determine which attributes, if any, are sufficiently diverse to merit more detailed examination in the future. Only floral hairs have been investigated more thoroughly.

Stems.—*Aneilema* stems are always succulent. Transverse sections of internodes of nine species, representing all sections of the genus, show a great similarity to one another. Their general structure is like that illustrated for *Commelina imberbis* by Tomlinson (1969:46, fig. 12). An outer cortex, varying in thickness according to species, is separated from an inner central cylinder by a continuous one-celled endodermis-like layer. The cortex lacks vascular bundles. Starting from the outside it comprises a thin cuticle, one-celled epidermis containing stomata, a zone of numerous alternating patches of collenchyma and chlorenchyma, and a narrow band of chlorenchyma, continuous with the subepidermal chlorenchyma patches. The central cylinder is composed of ground parenchyma with scattered vascular bundles.

Leaves.—Transverse sections of the leaves show a thin, smooth cuticle, an upper and lower epidermis usually composed of more or less isodiametric cells (cells elongate at right angles to the leaf surface occur in *A. succulentum* and *A. zebrinum*), and a relatively thin mesophyll composed of a single, adaxial palisade layer and an abaxial spongy mesophyll generally composed of three to four cell layers. A hypodermis is present only in the midrib region as two small, adaxial patches, one on either side of the midrib. The hypodermis is, in part, usually more than one cell layer thick. Collenchyma is present between the midrib and the lower epidermis (Tomlinson, 1969:40, fig. 10-1). The form and position of the hypodermis and collenchyma result in a more or less W-shaped mesophyll in the midrib region. A submarginal vein is present, but margin collenchyma and sclerenchyma are lacking. Silica is absent.

Raphides.—Raphides are present in most parts of the plant, including the anthers and root tips. According to Tomlinson (1966, 1969), the raphides occur in elongate raphide-sacs arranged in longitudinal series to form raphide canals. Fresh-cut shoots exude a sap that is sometimes slightly milky

due to the presence of abundant raphides.

STOMATA.—Stomata occur on all green parts of the plant. On the leaves they are always more abundant on the abaxial surface than the adaxial, on which occasionally they may be lacking. The stomata typically have six accessory or subsidiary cells, two lateral pairs and one terminal pair (Tomlinson, 1969:30, fig. 6). The stomata on the sepals are often less regular in accessory cell number, two to seven accessory cells having been observed.

HAIRS.—Hairs may occur on all aerial parts of the plant with the exceptions of the staminodes and medial stamen. Among the vegetative and reproductive organs, only the leaves and sepals always have hairs. The following hair types are recognizable (terminology partly after Tomlinson, 1966):

1. Glandular microhairs (Figures 40*a–c,i*, 42*a,b,h*): three-celled, appressed hairs, each with small basal and medial cells and an elongate, glandular apical cell. These may occur on all parts of the plant where hairs are found except the stamen filaments. They are particularly dense on the adaxial surface of the sepals, where they have been found in all 26 *Aneilema* species that have been checked for this character. Tomlinson (1966) reported that glandular microhairs on the vegetative organs vary little within each species. In contrast, the glandular microhairs, when present on the abaxial sepal surface, are always much smaller than those of the adaxial surface. Glandular microhairs are probably present in all *Aneilema* species.

2. Hook-hairs (Figures 40*d,e,j*, 41*g*, 42*j,m*): hairs in which the terminal cell is hooked. As defined by Tomlinson (1966), hook-hairs are always two-celled. In *Aneilema* that is true of all non-floral hook-hairs as well as some floral ones. However, some of the latter, which are also termed hook-hairs here, may have as many as five cells. Two-celled hook-hairs of two or more size classes occur on the vegetative and/or reproductive parts in some species of sections *Amelina* and *Brevibarbata* and some or all species of section *Pedunculosa* (Figure 40*d,e*). Hook-hairs occur on the leaves of all *Aneilema* species and in the inflorescences of all but a few species.

3. Prickle hairs (Figure 40*g*): two-celled hairs with a broad basal cell and short, stiff apical cell not exceeding the basal cell in length. These occur on the leaf margins of most *Aneilema* species. They are typically apically directed and make the margins scabrid. They sometimes also occur on the lamina surfaces, but are rare on other parts of the plant. They grade imperceptibly into the next hair type.

4. Uniseriate or acicular hairs (Figure 40*f*): two- to several-celled hairs with sharply pointed apical cells, when two-celled, the apical cell longer than the basal cell. These are the cilia on the sheath apex and frequently of the petiole and lamina margins of many *Aneilema* species. Uniseriate hairs are also frequent on the sheath and lamina surfaces. They are uncommon on the internodes and in the inflorescences and flowers. Their occurrence in the inflorescences is sometimes a diagnostic specific character. The distinction used here between two-celled uniseriate and prickle hairs is quite arbitrary. Further studies may suggest that the two should be separated at a different level.

5. Uniseriate-eglandular hairs (Figure 41*a–c,e,h*): two- to six-celled hairs differing from uniseriate hairs in having rounded apical cells. These are found only on lateral stamen filaments, occurring in all species (as far as is known) of sections *Brevibarbata* and *Pedunculosa* and in *A. nyasense* of section *Amelina*.

6. Uniseriate-glandular hairs (Figures 40*h*, 41*f*, 42*c–g,i,k,l,n,o*): three- to six-celled hairs in which the apical cell is glandular. The three-celled ones (Figure 42*d*) differ from glandular microhairs, from which they are probably derived, in having much stronger basal cells and small apical cells. Uniseriate-glandular hairs are confined to the flowers, being common on the ovaries and rare on the petals (only in *A. aequinoctiale*) and lateral stamen filaments (only in *A. gillettii*). These hairs may be further subdivided on the basis of whether or not the apical cell is capitate.

7. Branched hairs (Figure 41*d*): four- to five-celled, eglandular hairs known only from the stamen filaments of *A. nyasense*.

The diversity of floral hairs suggested that these might be diagnostic at the specific or sectional ranks. The floral hairs of 19 species, representing all seven sections of the genus, were studied in detail. The distribution of the different hair types within these species is shown in Tables 3–5. The results support the morphological and cytological data indicating that sections *Aneilema*, *Rendlei*, *Lamprodithyros*, and *Pedunculosa* are natural, while sections *Amelina* and *Brevibarbata* may not be natural. *Aneilema somaliense* of section *Somaliensia* is separable from all of the above by a combination of characters, but no light has been shed on the naturalness of section *Somaliensia* as a whole. Floral hairs also appear to be useful at the specific level in many instances.

Vegetative hairs and anatomy seem to be of more limited use, but detailed studies of epidermal patterns and of the distribution of hairs on the lamina may be worthwhile in certain critical species complexes, e.g., *A. beniniense*, *A. umbrosum*, and *A. welwitschii*.

It is not yet clear whether *Aneilema* can be distinguished anatomically from all other genera of Commelinaceae. It appears that at least the closely related genus *Rhopalephora* is probably not separable on anatomical characters alone.

Cytology of *Aneilema*

Chromosome numbers and chromosome morphology of *Aneilema* species were studied extensively by Faden and Suda, and their findings, as well as a summary of all previous counts, were included in Faden (1975). Several counts from this survey were published in Faden (1983b). Along with data accumulated since, the complete results will be published separately.

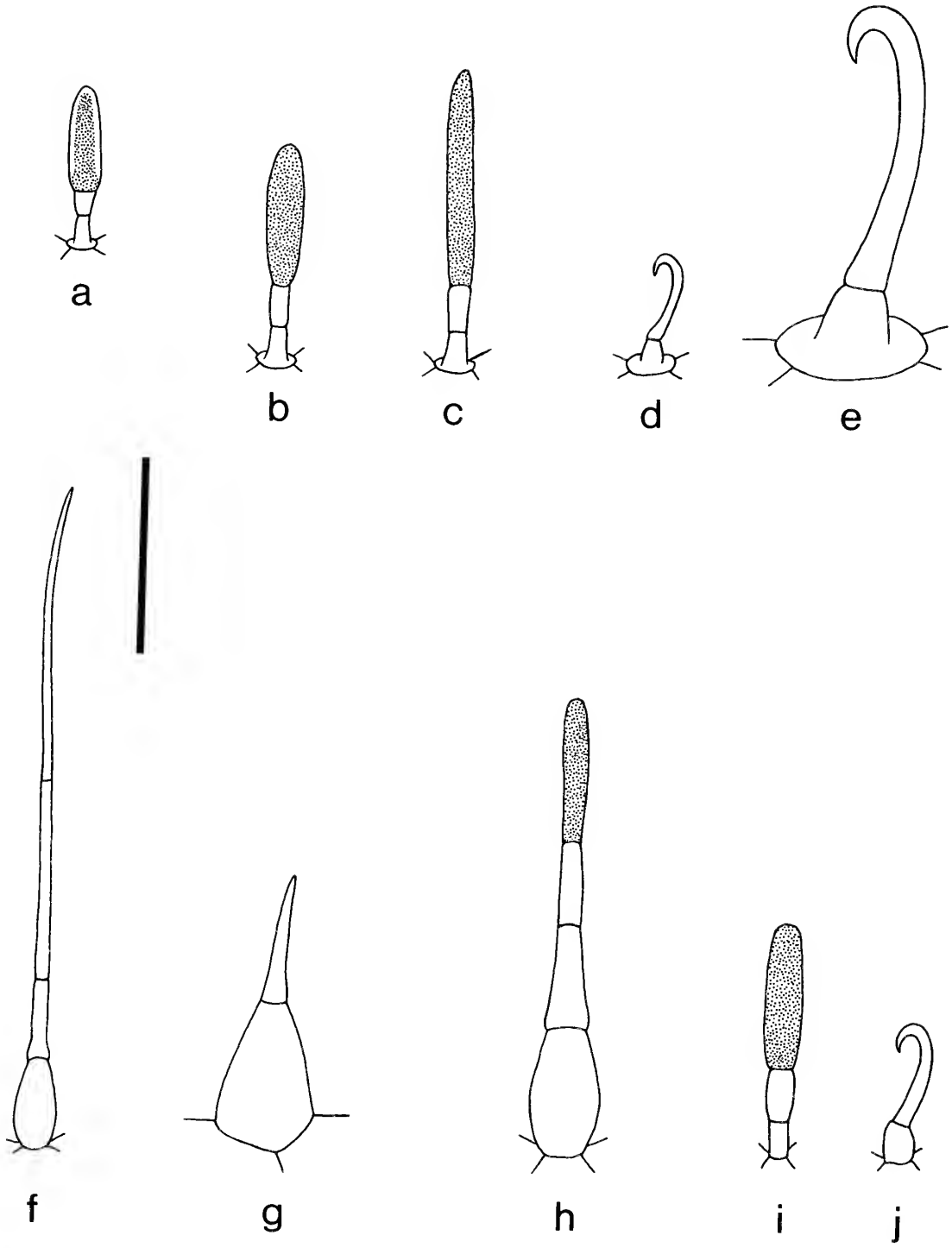


FIGURE 40.—Sepaline and petaline hairs in *Aneilema*. Sepaline hairs (*a–g*): (*a–c*, adaxial glandular microhairs): *a*, *A. biflorum* R. Brown (from *Tindale in NSW84495*); *b,c*, *A. beniniense* (P. de Beauvois) Kunth (from *Faden et al. 74/71*); (*d,e*, hook-hairs): *A. hockii* De Wildeman (from *Faden et al. 72/234*); *f*, acicular hair, *A. hirtum* A. Richard (from *Paget-Wilkes B*); *g*, prickle hair, *A. zebrinum* Chiovenda (from *Faden et al. 74/330*). Petaline hairs (*h–j*): *h*, uniseriate-glandular hair, *A. aequinoctiale* (P. de Beauvois) G. Don (from *Faden et al. 71/922*); *i*, glandular microhair, *A. ephemerum* Faden (from *Faden & Faden 74/794*); *j*, hook-hair, *A. ephemerum* Faden (from *Faden & Faden 74/794*). (Bar = 0.1 mm for *a–e,g–j;* 0.3 mm for *f*.)

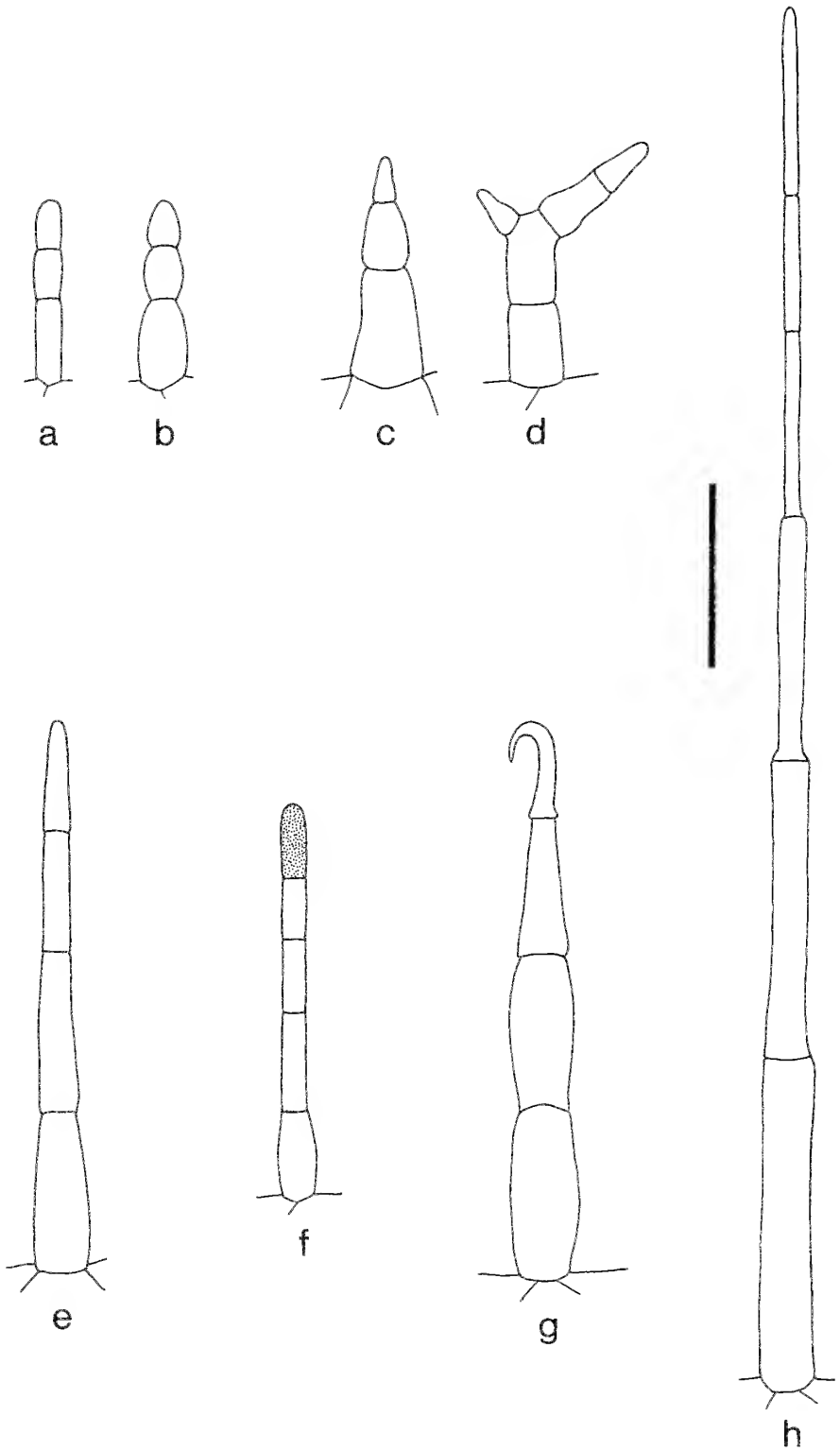


FIGURE 41.—Stamen filament hairs in *Aneilema*. (*a–c,e,h*, uniseriate-eglandular hairs): *a, b, A. beniniense* (P. de Beauvois) Kunth (from *Faden et al. 74/71*); *c, A. nyasense* C.B. Clarke (from *Faden et al. 69/1092*); *e, A. brunneospermum* Faden (from *Faden et al. 74/209*); *h, A. hirtum* A. Richard (from *Paget-Wilkes B*); *d*, branched hair: *A. nyasense* C.B. Clarke (from *Faden et al. 69/1092*); *f*, uniseriate-glandular hair: *A. gillettii* Brenan (from *Friis 1044*); *g*, hook-hair: *A. aequinoctiale* (P. de Beauvois) G. Don (from *Faden et al. 71/922*). (Bar = 0.1 mm.)

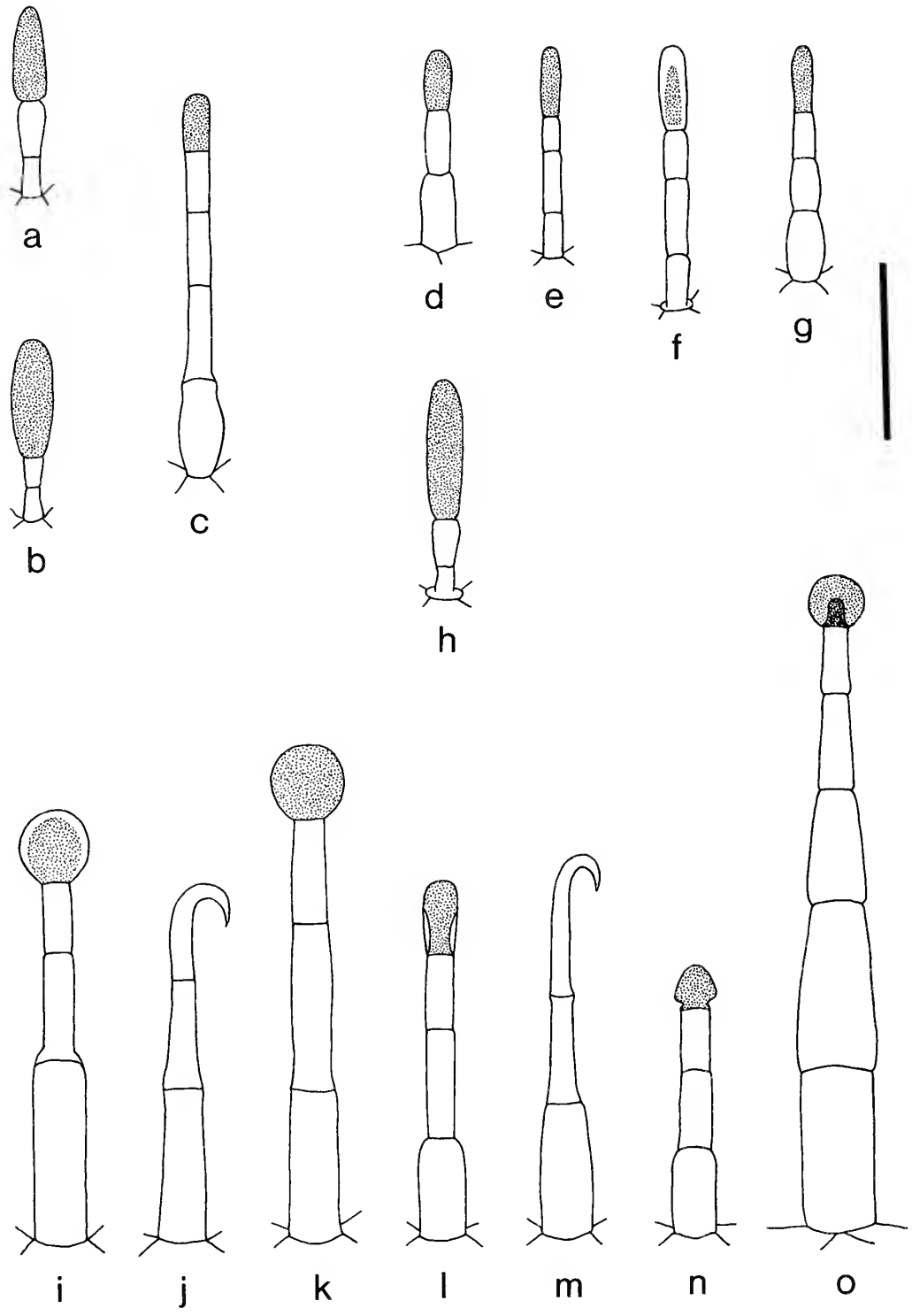


FIGURE 42.—Ovarian hairs in *Aneilema*. (*a,b,h,* glandular microhairs): *a, A. rendlei* C.B. Clarke (from *Faden & Faden 72/240*); *b, A. taylorii* C.B. Clarke (from *Faden & Faden 74/371*); *h, A. johnstonii* K. Schumann (from *Faden et al. 71/907*); (*c-g,i,k,l,n,o,*) uniseriate-glandular hairs: *c, A. somaliense* C.B. Clarke (from *Faden & Faden 74/923*); *d, A. nyasense* C.B. Clarke (from *Faden et al. 69/1092*); *e, A. ephemerum* Faden (from *Faden & Faden 74/794*); *f, A. hockii* De Wildeman (from *Faden et al. 72/234*); *g, A. aequinoctiale* (P. de Beauvois) G. Don (from *Faden et al. 71/922*); *i, A. clarkei* Rendle (from *Evans & Maikweki 51*); *k, A. recurvatum* Faden (from *Faden et al. 69/1066*); *l, A. zebrinum* Chiovenda (from *Faden et al. 74/330*); *n, A. brunneospermum* Faden (from *Faden et al. 74/209*); *o, A. hirtum* A. Richard (from *Paget-Wilkes B*); (*j,m,* hook-hairs): *j, A. clarkei* Rendle (from *Evans & Maikweki 51*); *m, A. zebrinum* Chiovenda (from *Faden et al. 74/330*). (Bar = 0.1 mm.)

TABLE 3.—Types and distribution of hairs on sepals in 19 species of *Aneilema* (figures refer to number of cells in the hairs; only presence (+) or absence (-) has been indicated for glandular microhairs because, by definition, they are always 3-celled).

Aneilema sections and species	Adaxial glandular microhairs	Abaxial			
		Glandular microhairs	Acicular or prickle hairs	Hook-hairs	
				Uniform in size	Two sizes
Section *Aneilema*					
A. neocaledonicum	+	-	-	-	-
A. acuminatum	+	-	-	-	-
A. biflorum	+	-	-	-	-
Section *Amelina*					
A. johnstonii	+	-	-	-	-
A. gilletii	+	+	-	2	-
A. hockii	+	+	-	-	2
A. aequinoctiale	+	+	-	-	2
A. ephemerum	+	+	-	-	2
A. nyasense	+	+	-	-	2
Section *Rendlei*					
A. taylorii	+	-	-	-	-
A. rendlei	+	-	-	-	-
Section *Somaliensia*					
A. somaliense	+	+	-	2	-
Section *Lamprodithyros*					
A. clarkei	+	-	-	2	-
A. recurvatum	+	+	-	2	-
A. zebrinum	+	+	2	2	-
Section *Brevibarbata*					
A. beniniense	+	-	-	-	-
A. brunneospermum	+	+	-	2	-
Section *Pedunculosa*					
A. hirtum	+	+	(±)4	-	2
A. termitarium	+	+	-	-	2

Chromosome numbers have been found to be very useful in delimiting the sections of *Aneilema* and in understanding some species and infraspecific taxa. The basic numbers obtained for each section are included in the descriptions of the sections. Chromosome counts for species of sections *Rendlei, Somaliensia,* and *Lamprodithyros* are listed in the accounts of these species. Because the full data will be presented elsewhere, only a brief summary will be included here.

Five basic chromosome numbers were mentioned for *Aneilema* by Faden and Suda (1980); a sixth has been found subsequently among the more than 40 species of the genus that we have counted: $x = 9$, 10, and 13–16. The sections that appear to be natural on morphological grounds usually have a single basic number, except section *Somaliensia:* section *Aneilema* ($x = 16$); section *Rendlei* ($x = 16$); section *Somaliensia* ($x = 14$, 16); section *Lamprodithyros* ($x = 13$); section *Pedunculosa* ($x = 9$). The remaining two sections are much more diverse in their morphology, and this is also reflected in their cytology: section *Amelina* ($x = 13$, 15, 16); section *Brevibarbata* ($x = 10$, 13, 15). The chromosomes of *Aneilema* are generally small and, in nearly all species, all or most chromosomes are metacentrics and submetacentrics.

Phytochemistry of *Aneilema*

Very little work has been done on the phytochemistry of *Aneilema*. Flavonoids are the only group that has been studied, as part of a general survey of these compounds in the Commelinaceae (Martinez and Swain, 1985). Twenty-four populations of 17 species, representing all seven sections of the genus, were examined. Flavone C-glycosides, the most common flavonoids in the family, were found in every population and were the only kinds of flavonoids present. Although the specific flavone C-glycosides found in each species are not listed, it would appear that flavone C-glycosides are of such wide distribution within the family and within *Aneilema* as to be worthless taxonomically.

Reproductive Biology of *Aneilema*

The only paper dealing extensively with the reproductive biology of *Aneilema* is that of Faden (1983b) in which the floral characters of five species from a single locality in Kenya are compared. Those data are in turn only a distillation of a great body of information that was accumulated from the field and from greenhouse observations and experiments in the course of

TABLE 4.—Types and distribution of hairs on the petals and stamen filaments in 19 species of *Aneilema* (figures refer to number of cells in the hairs; only presence (+) or absence (–) has been indicated for glandular microhairs because, by definition, they are always 3-celled).

Aneilema sections and species	Petals			Stamen filaments			
	Glandular microhairs	Hook-hairs	Uniseriate-glandular	Hook-hairs	Uniseriate-eglandular	Uniseriate-glandular	Branched
Section *Aneilema*							
A. neocaledonicum	–	–	–	–	–	–	–
A. acuminatum	–	–	–	–	–	–	–
A. biflorum	–	–	–	–	–	–	–
Section *Amelina*							
A. johnstonii	–	–	–	–	–	–	–
A. gillettii	–	–	–	–	4–6	4–6	–
A. hockii	–	–	–	–	–	–	–
A. aequinoctiale	–	3–4	3–5	3–5	–	–	–
A. ephemerum	+	2	–	–	–	–	–
A. nyasense	–	–	–	–	2–5	–	4–5
Section *Rendlei*							
A. taylorii	–	–	–	–	–	–	–
A. rendlei	–	–	–	–	–	–	–
Section *Somaliensia*							
A. somaliense	–	–	–	–	–	–	–
Section *Lamprodithyros*							
A. clarkei	–	–	–	–	–	–	–
A. recurvatum	–	–	–	–	–	–	–
A. zebrinum	–	–	–	–	–	–	–
Section *Brevibarbata*							
A. beniniense	–	–	–	–	2–3	–	–
A. brunneospermum	–	–	–	–	3–6	–	–
Section *Pedunculosa*							
A. hirtum	–	–	–	–	5–6	–	–
A. termitarium	–	–	–	–	4–6	–	–

preparation of Faden (1975) and subsequently. Because a compilation of all these data is likely to be overlooked in a work that is largely taxonomic, only a summary will be included here, and the rest will be published elsewhere.

Aneilema species differ from one another in a number of features of floral structure and biology that may be important for pollination and reproductive isolation. Among the biologically significant morphological characters are types of flowers present, flower size, petal color, position of the stamens at anthesis, pubescence of the lateral stamen filaments, fertility of the pollen in the different anthers, and stigma position relative to that of the anthers. The variation in these characters within *Aneilema* is discussed under "Reproductive Morphology," above. Floral reproductive attributes, other than strictly structural ones, that may also be important are presence or absence of a scent, daily flowering times, retention of the lateral stamens by the medial petal, and presence or absence of self-compatibility and autogamy.

One hundred and eighty-four insects and two spiders were collected on or associated with 18 *Aneilema* species in six African countries (Ghana, Zambia, Malawi, South Africa, Kenya, and Tanzania) in 1974. The major insect orders collected were (1) Hymenoptera (79 individuals)—Megachilidae: two genera (at least four species); Halictidae: three genera (at least three species); Anthophoridae: seven genera (at least nine species); Apidae: two genera (at least two species); (2) Diptera (42 individuals)—Sciaridae: one genus (two species); Bombydiidae: two genera and species; Syrphidae: eight genera (at least eight species); Calliphoridae: one genus and species; (3) Coleoptera (53 individuals)—Scarabaeidae: two genera and species; Dermestidae: one genus and species; Melyridae: one genus and species; Meloidae: two genera (at least five species); Alleculidae: one genus and species; Chrysomelidae: five genera (at least nine species). Other insect orders collected were Hemiptera (four individuals), Thysanoptera (one) and Lepidoptera (five larvae).

Despite this large set of data, few generalizations can be made. To some degree, the numbers and diversity of insects collected from an *Aneilema* species seem to be correlated with the number and length of the observation periods, the number of different populations of the species sampled, and the size of the population or populations. It also appears that a combination of *Aneilema* species and, especially, the presence of a nectar source, such as species of *Plectranthus* (Lamiaceae), in

TABLE 5.—Types and distribution of hairs on the ovary in 19 species of *Aneilema* (figures refer to number of cells in the hairs; only presence (+) or absence (–) has been indicated for glandular microhairs because, by definition, they are always 3-celled).

Aneilema sections and species	Glandular microhairs	Prickle hairs	Hook-hairs	Uniseriate-glandular	
				Capitate	Non-capitate
Section *Aneilema*					
A. neocaledonicum	–	–	–	–	–
A. acuminatum	–	–	–	–	–
A. biflorum	–	–	–	–	–
Section *Amelina*					
A. johnstonii	+	–	–	–	–
A. gillettii	–	–	2	–	4–6
A. hockii	–	–	–	–	4
A. aequinoctiale	–	–	–	–	4
A. ephemerum	–	–	–	–	4
A. nyasense	–	–	–	–	3–4
Section *Rendlei*					
A. taylorii	+	–	–	–	–
A. rendlei	+	–	–	–	–
Section *Somaliensia*					
A. somaliense	–	–	(±)3	–	5–6
Section *Lamprodithyros*					
A. clarkei	–	–	3	4	–
A. recurvatum	–	–	–	4	–
A. zebrinum	–	2	2–3	–	3–4
Section *Brevibarbata*					
A. beniniense	–	–	–	–	–
A. brunneospermum	–	–	–	4	–
Section *Pedunculosa*					
A. hirtum	–	–	–	6	–
A. termitarium	–	–	–	5–6	–

the vicinity may increase the number of insect species visiting particular *Aneilema* species. Among the 18 *Aneilema* species on which insects were caught, only *A. petersii* subsp. *pallidiflorum* and *A. hockii*, growing in the Tsavo area of Kenya, could be considered relatively well sampled. The largest numbers of insect species were collected on these taxa: *A. petersii* subsp. *pallidiflorum* (six Hymenoptera species, three Diptera, five Coleoptera, one Lepidopteran); *A. hockii* (six Hymenoptera, six Coleoptera). The single, large population of *A. nicholsonii*, which was visited only once, yielded two species of Hymenoptera, four Diptera, three Coleoptera, and one Thysanopteran.

In contrast to these data, a month-long, intensive study of the reproductive biology of *Commelina erecta* L. in Texas in 1981 yielded 44 visiting insect species (Faden, unpublished). Because no *Aneilema* species was intensively studied for that length of time, one might expect that more insect visitors could have been obtained from further observations of even the best sampled *Aneilema* species.

Two further generalizations may be made. Larger flowers, such as those of *A. hockii*, tend to attract larger bees than smaller flowers, e.g., *A. succulentum*. This is especially true if the stamens of the larger flower extend forwards to a considerable degree rather than bend downwards (Faden, 1983b). Finally, most *Aneilema* species seem to be visited (and presumably pollinated) chiefly by bees. Bees were collected on 16 *Aneilema* species and flies (mostly Syrphidae) on only eight species; both bees and flies were collected on seven species. It is noteworthy that equal or greater numbers of fly than bee species were obtained from only five *Aneilema* species. These species (*aequinoctiale, welwitschii, nicholsonii, pedunculosum,* and *spekei*) all have bearded filaments, and they include all three species of section *Pedunculosa* (*nicholsonii, pedunculosum, spekei*) and the only species of section *Amelina* (*aequinoctiale*) with bearded filaments on which insects were collected. These four species all have longly bearded filaments, unlike the short-bearded *A. welwitschii* (section *Brevibarbata*). Only a single fly and no bees were collected on the last species.

In contrast to the above, 10 of the 12 *Aneilema* species on which more bee than fly species were collected have glabrous filaments, and the other two have shortly bearded ones. The glabrous-filament species include all seven species of section *Lamprodithyros* (*calceolus, clarkei, indehiscens, lamuense, petersii, succulentum, tanaense*), both glabrous-filamented

species of section *Amelina* (*hockii, johnstonii*), and the only species of section *Rendlei* (*rendlei*) that were sampled. The two bearded-filamented species (*arenicola, umbrosum* subsp. *umbrosum*) both belong to section *Brevibarbata*. On *A. arenicola* only a single bee and no flies were collected.

From these data it may be concluded that flies, particularly Syrphidae, are attracted to and probably serve as the chief pollinators for *Aneilema* species with longly bearded stamen filaments; that bees are the main pollinators of the glabrous-filament species and possibly some short-bearded-filament species; and that the data for short-bearded-filament species is too inadequate to generalize about this group of species. The data for the three species of section *Amelina* are especially instructive: the two species with glabrous filaments are visited mainly by bees; the single species with long-bearded filaments is visited predominantly by flies.

The occurrence of Coleoptera does not seem to follow any taxonomic or clear morphological pattern within *Aneilema*—perhaps the data are too incomplete—and it is probable that the beetles are merely feeding on the flowers, although some of them may occasionally effect pollination.

Pollination of related, co-occurring species of *Aneilema* by different pollinators can lead to reproductive isolation. In a colony of five species, *A. succulentum* was found to not share any pollinators with the other species (Faden, 1983b).

There are two pollination syndromes that require comment. In most species of section *Lamprodithyros*, the large medial petal retains the lateral stamens when the flowers opens, only releasing them when the margins of this petal uncurl (see "Reproductive Morphology," above, and Faden, 1983b). The stamen retention mechanism may promote outerossing by the presentation, when a flower first opens, of only part of the flower's total pollen to the pollinator, thereby forcing the insect to visit more flowers. The same mechanism may also prolong the period during which the flower can attract insects by the release of a second source of pollen—that of the lateral anthers—after the pollen of the medial stamen anther, which is always free, may have already been collected.

Within section *Lamprodithyros*, there is much variation in the degree of development of the stamen retention mechanism. In species such as *A. petersii* and *A. indehiscens*, this syndrome appears to be primitively lacking; in *A. tanaense, A. calceolus,* and *A. recurvatum*, it is well developed; in *A. succulentum* it is poorly developed and perhaps disappearing; and in *A. zebrinum* it seems to have been lost entirely. These different degrees of development of this mechanism, perhaps in combination with differences in flowering times, may result in reproductive isolation between related species (Faden, 1983b).

The other syndrome of note is automimicry in *A. rendlei* and *A. brenanianum*. In those species the perfect and staminate flowers are the most dimorphic in the genus. The lateral stamens of the staminate flower are held close together in the same position as the style in the perfect flower, which they closely resemble in color, shape, and curvature, and so the two flower types strongly resemble one another (Figure 17*a,b;* Plate 2*b,d*). In *A. rendlei* it has been observed that the main insect visitors and presumed pollinators are workers of a very small, black bee (*Trigona* species). The bees have been observed to first land on the very prominent medial anther, collect pollen from it, and then, in the staminate flowers, to climb down the filaments of the lateral stamens in order to collect pollen from those anthers. In the field it has been observed that in populations of *A. rendlei*, staminate flowers are much more numerous than perfect flowers. Thus I believe that the bees are conditioned to the described behavior pattern, which they repeat when they visit perfect flowers and thereby transfer pollen to the stigma, with which they would otherwise not make contact because of the bees' diminutive size.

All *Aneilema* species have characteristic daily flowering times (Figure 25). In cultivation it has been observed that these times may vary somewhat, according to the ambient temperature, but the range of variation is normally quite small. I have noted in Faden (1983b) that flowering times in related, co-occurring species, e.g., *A. petersii* and *A. succulentum*, may be totally non-overlapping, thus preventing any gene exchange between the species.

Aneilema flowers differ from those of some other genera of Commelinaceae, e.g., *Commelina*, in that the style does not roll up within the other floral parts when the flower fades. Thus, if the anthers are not in contact with or very close to the stigma when the flower is fully open, the flower will not self-pollinate, even in demonstrably self-compatible species such as *A. rendlei*. The species with autogamous flowers probably include all of the annuals in addition to many perennials such as *A. umbrosum* and *A. zebrinum*. Perennials, in addition to *A. rendlei*, that are not autogamous include *A. hockii* and *A. johnstonii*. Annual populations of *A. tanaense*, which have been observed in cultivation, regularly show autogamy. In contrast, a single perennial population of the same species, which has been cultivated for 10 years, has never set fruit without being intentionally pollinated.

Self-compatibility at the level of the stigma and pollen grain in *Aneilema* has been reported on only by Owens (1981), who recorded all five species that he tested (*A. aequinoctiale, A. brenanianum, A.* sp. aff. *spekei, A. zebrinum, A.* sp.) as self-compatible. I have tried to determine compatibility by noting whether self-pollination leads to fruit set and and seed development. The results reported in Faden (1983b) (*A. hockii*, self-incompatible; *A. petersii* subsp. *petersii, A. indehiscens* subsp. *indehiscens*, and *A. succulentum*, possibly self-incompatible; and *A. tanaense*, self-compatible) were obtained in that way. Among those species, experimental pollinations were performed only on *A. hockii* and *A. tanaense*, hence the uncertainty about situation in the other taxa.

There are no published data on seed dispersal in *Aneilema*. In general, the capsules and seeds do not show any clear adaptations for dispersal. Usually only one type of diaspore is produced, the individual ventral locule seeds, but in some species, e.g., *A. pusillum* and *A. petersii* (see "Reproductive Morphology, Capsules," above), a second type of disseminule,

the deciduous, dorsal capsule valve containing the single, dorsal locule seed, is also formed. One may speculate that these two types of disseminules are dispersed by different means, particularly in species of section *Lamprodithyros,* where the dorsal and ventral locule seeds themselves may be strongly dimorphic. In *A. tanaense* a small number of hook-hairs is present on the dorsal valve, suggesting possible exozoochory (Faden, unpublished). It has also been found that the strongly dimorphic seeds in this species have different germination patterns (Faden and Teeri, unpublished).

Taxonomy of *Aneilema*

Introduction to Taxonomy

The taxonomic treatment used here is based upon a study of a wide range of herbarium specimens (see "Acknowledgments") and, when available, living plants and preserved materials (see "Materials and Methods"). All *Aneilema* taxa have been investigated, and all types, except for the few destroyed during the Second World War, have been examined. This phase of the research led to an initial determination of species limits and synonymy. The list of species, thus established, has been used as a working hypothesis, being revised when necessary. It must still be considered tentative for those sections of the genus not thoroughly revised in the present study. Species recognized as distinct but undescribed were given specific names in Faden (1975), so they could be referred to readily. Some have been described subsequently (Faden, 1978a, 1984). Most of the others are described in this work; the remaining few will be formally described in future papers under the specific names used here.

The large size of the genus prevented a study of all species in sufficient detail to understand their total variation. Therefore, once sectional limits were established, three sections were selected for more intensive investigation. Sections *Rendlei* and *Lamprodithyros* were chosen because large percentages of the taxa in each were known from living material, having been observed in the field and maintained in cultivation. Section *Somaliensia* was selected because its thitherto poorly known species had to be thoroughly examined anyway, in order to delimit the section.

Keys to all species have been included. Those to the species in the four sections that have not been thoroughly revised should be considered provisional.

In order that no true *Aneilema* species might be overlooked among the 260 names that have been included in the genus (see Appendix II), types for most of these epithets have been examined. Particular emphasis has been placed on those taxa whose generic position was considered uncertain by Morton (1966) and whose geographic distributions and descriptions suggested possible valid inclusion in *Aneilema,* e.g., the Madagascan species of Perrier de la Bâthie (1936, 1938). The few specific epithets in *Aneilema* for which the exact generic position has not been determined are very unlikely to belong to this genus, on the basis of their distributions and, in some cases, their descriptions.

Taxonomic Units

The species concept used here is fundamentally a taxonomic one (Davis and Heywood, 1964:91), the species being distinguished primarily on the basis of morphological discontinuities.

Whenever possible an attempt has been made to refine the species limits, initially established on morphological criteria, through consideration of other kinds of data, such as distribution, ecology, phenology, breeding systems, karyotypes, and the result of crosses. The inclusion of such data has confirmed the preliminary taxonomic decisions in nearly all cases. Where the morphological data have not been supported by the biological data, the relative importance of each has had to be judged on a case-by-case basis. It is hoped that the use of a wide variety of characters in the final determination of specific limits will have made the resulting taxonomy as natural as possible within the bounds of the present state of our knowledge of these plants.

Subspecies as used here may be defined as geographic segregates of a species that differ from one another in relatively few morphological characters. The morphological attributes that separate subspecies are presumed to not be in themselves of sufficient magnitude to prevent interbreeding. Subspecies may differ in biological characters, however, such as ploidy, that can be expected to have a more profound effect on potential gene exchange than their morphological differences. The ranges of subspecies may be discrete or overlapping.

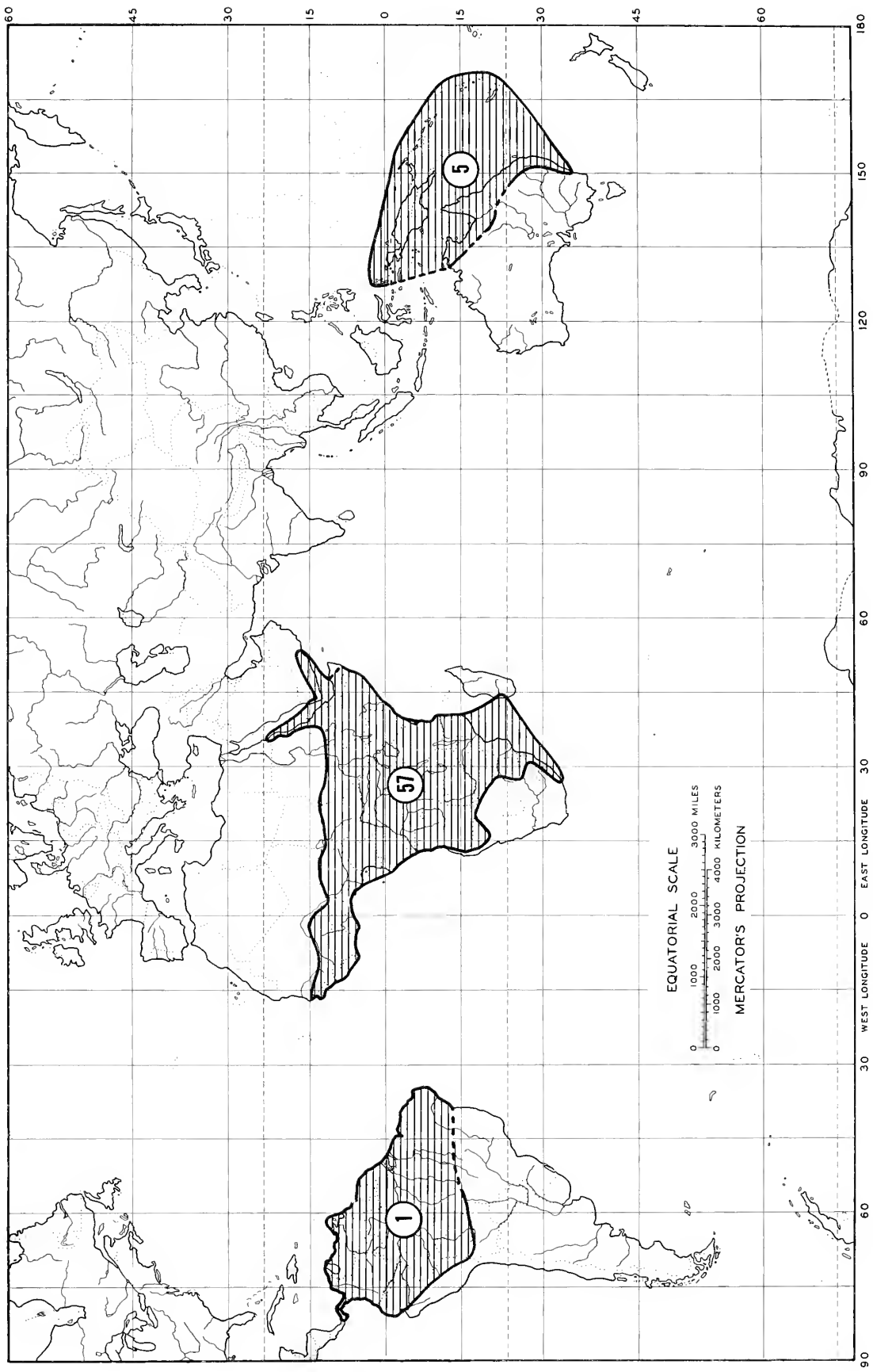
Varieties have not been used in the present treatment because the distinction between local variants, perhaps worthy of taxonomic rank, and odd specimens, not meriting formal recognition, is seldom clean-cut in *Aneilema.* Minor variants and unusual specimens are dealt with in the discussion of each species.

Distribution of *Aneilema*

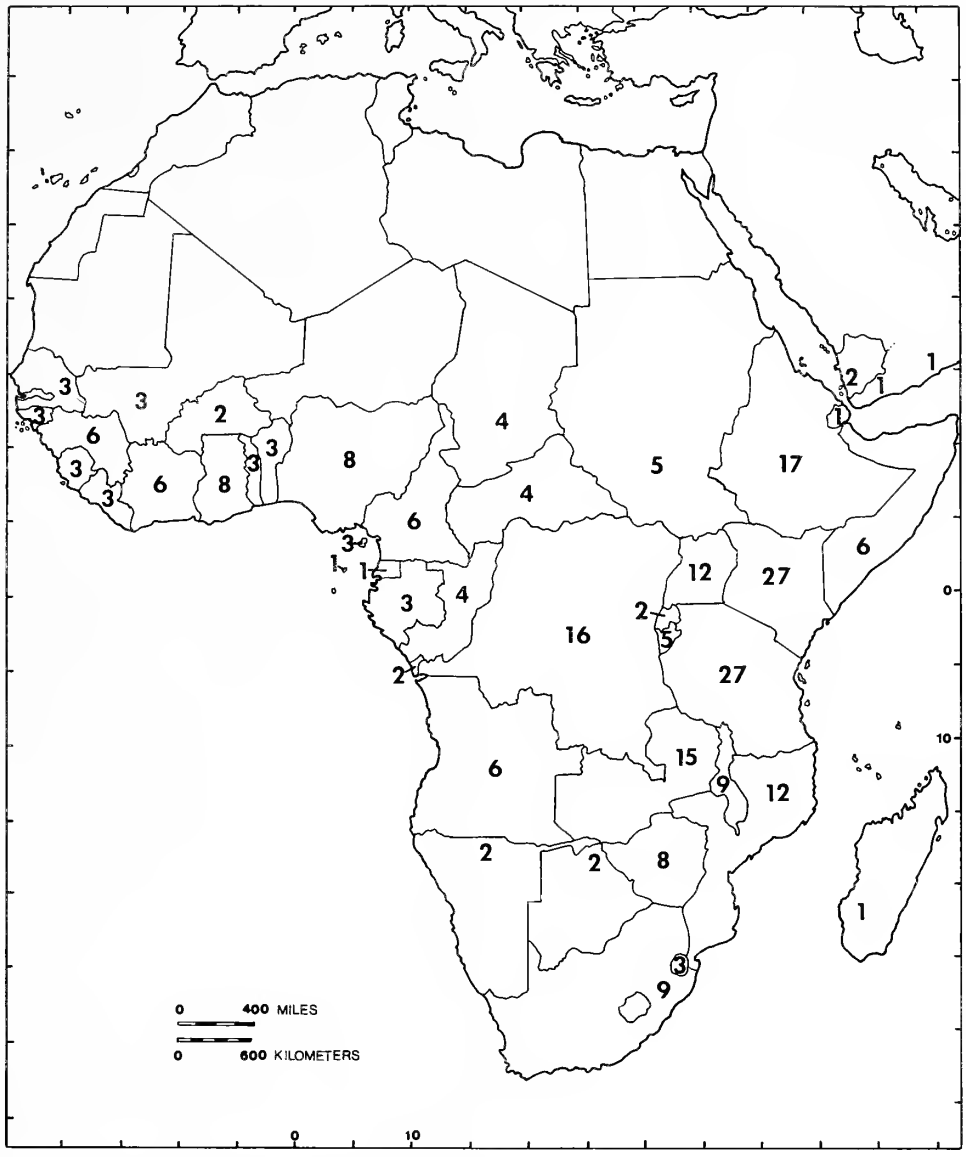
The genus *Aneilema* contains 62 species and occurs in three regions: eastern and northern Australia and the surrounding islands; tropical and subtropical Africa, Madagascar, and southern Arabian Peninsula; and tropical America (Map 1). Its absence from Asia except for two species occurring near the Red Sea is noteworthy.

Aneilema is best represented in Africa with about 55 species, one of which extends to the Arabian Peninsula. One species is endemic to Madagascar and another to the Yemen Arabic Republic. Five species, all endemic, occur in the Australian region and only one in the neotropics. The latter, *A. umbrosum,* also occurs in Africa.

Of the five Australo-Oceanic species, three are endemic to Australia, one (*A. neocaledonicum*) is confined to New Caledonia and adjacent islands, and the fifth (*A. acuminatum,*



MAP 1.—Distribution of *Aneilema* R. Brown. The numbers represent the number of species in each of the three major geographic regions.



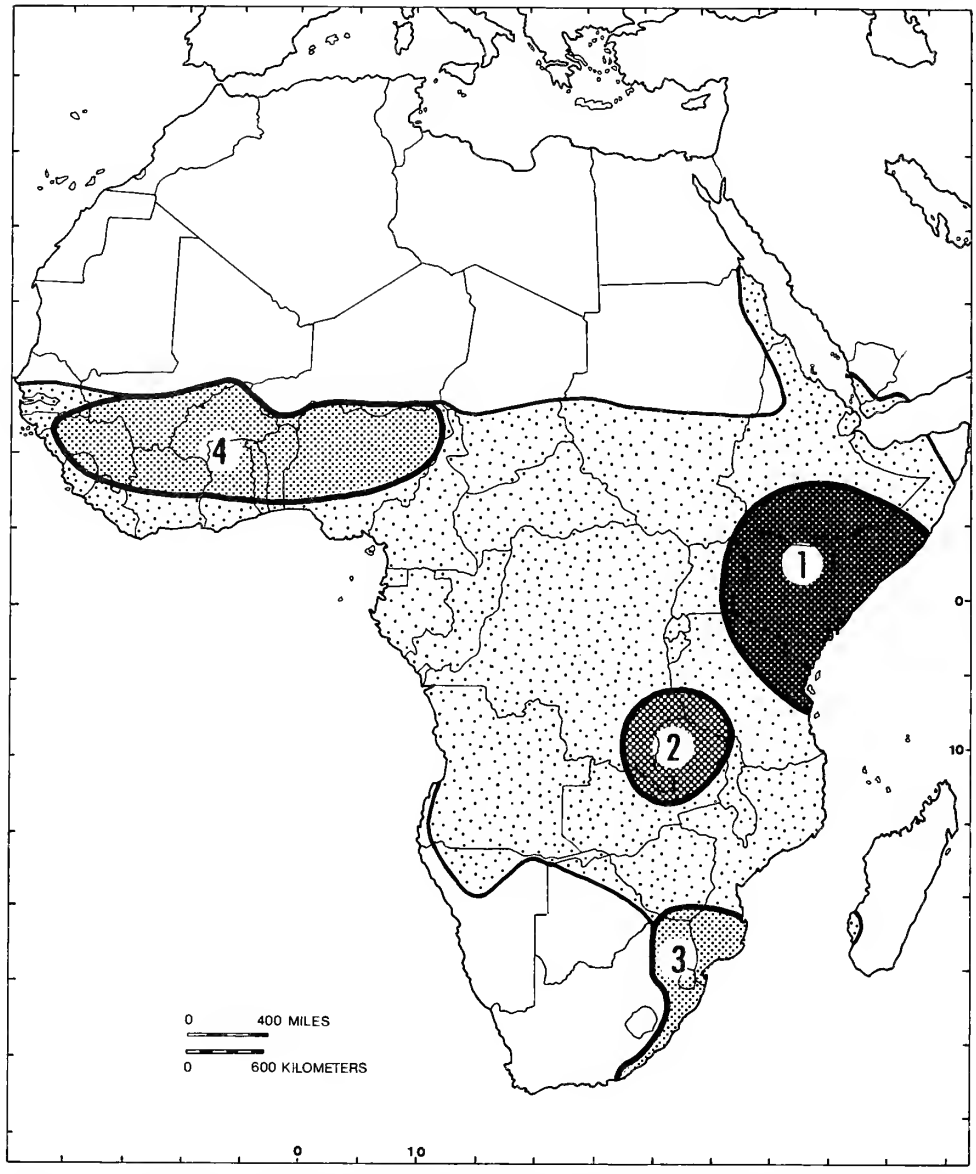
MAP 2.—Numbers of *Aneilema* species in African countries.

including *A. papuanum*) occurs throughout the region with the exception of New Caledonia.

The number of *Aneilema* species in different parts of Africa shows considerable variation. The number of species per country is shown in Map 2. The greatest diversity of species is in the East African region extending from southern Ethiopia and central Somali Republic south to central Tanzania. Thirty-five species occur of which 18 are endemic to the region. A secondary concentration (15 species including five endemics) is located in southwestern Tanzania, southeastern Zaire, and northern Zambia. Another region of relatively high endemism (nine species, five endemic) occurs in southern Mozambique and southwestern Zimbabwe south to northern and eastern Transvaal and northeastern Cape Province, South Africa. The fourth such concentration is in the savannah region of West Africa (Sierra Leone and Senegal to Chad), where seven species (four endemic) occur. The species of this region include several very distinctive, infraspecific taxa, e.g., *A. paludosum* A. Chevalier subsp. *pseudolanceolatum* J.K. Morton, that may prove worthy of specific rank.

It is significant that all four regions of relatively high species endemism (Map 3) are predominantly non-forested areas. The Congo Forest itself contains only five to six *Aneilema* species, most of which have wide ranges.

All seven sections of *Aneilema* recognized herein occur in Africa or Madagascar. Section *Aneilema*, which includes all of the Australian species, is represented in the African region solely by the Madagascan endemic *A. aparine*. The remaining



MAP 3.—Concentrations of *Aneilema* species in Africa: 1, East African center; 2, Zambian center; 3, Mozambique-South African center; 4, West African center. The shading is approximately proportional to the number of species in each area (see text).

six sections are exclusively or predominantly African. All six have species in the East African center of diversity. Sections *Rendlei* and *Somaliensia* are wholly or largely confined to this region of endemism, while sections *Amelina* and *Lamprodithyros* include species endemic to it. The Zambian center contains species of sections *Amelina, Brevibarbata,* and *Pedunculosa* and endemics of the latter two. The Mozambique-South African center is comprised of species of sections *Amelina, Brevibarbata,* and *Lamprodithyros* including endemics of the first two. All of the species of the West African savannah region belong to section *Brevibarbata.*

The distribution of *Aneilema* is unique in the Commelinaceae. Only five other genera (*Buforrestia, Commelina, Floscopa, Murdannia, Pollia*) occur in both the Eastern and Western Hemispheres (Faden, 1978c, 1983a). Among them, *Buforrestia* is confined to Africa and South America. The other four occur in Australia, like *Aneilema,* but their ranges extend beyond that of the latter. *Commelina* is more or less cosmopolitan but best represented in Africa; *Murdannia* and *Pollia* are chiefly tropical and subtropical Asiatic, and *Floscopa* is primarily African but is also present in tropical Asia. It is significant that all six genera that occur in Africa and tropical America are better represented in the former, suggesting a dispersal from Africa to the neotropics (Raven and Axelrod, 1974). This is certainly correct for *Aneilema.* No genus is present in both Australia and Africa that does not also

occur in the neotropics.

Among the 17 genera of Commelinaceae that occur in Africa and/or Madagascar, only *Commelina* has a distribution and concentration of species similar to that of *Aneilema*. Like that genus, *Commelina* contains relatively few forest species, the bulk of its taxa occurring in woodland, grassland, and bushland habitats. Although well represented in all four African regions in which *Aneilema* has concentrations of species, *Commelina* appears to have its greatest diversity in the Zambian region rather than in East Africa.

Besides *Aneilema* and *Commelina*, only *Floscopa* among African Commelinaceae includes both forest and non-forest species. Unlike them, it occurs in primarily aquatic habitats. Its greatest concentration of species is in West Africa, with a secondary center in the Zambian region. In the East African and Mozambique-South African regions (as defined above) *Floscopa* is represented by a single widespread species, *F. glomerata* (J.A. & J.H. Schultes) Hasskarl.

History and Typification of *Aneilema*

The nomenclatural history of the genus *Aneilema* has been described in detail elsewhere (Faden, 1978b) and need only be summarized here. The genus was described by Robert Brown (1810) for 10 Australian species that are now recognized as belonging to three genera. The genus was considered synonymous with *Commelina* by most workers until Kunth (1843) recognized it. Between 1843 and 1881 a number of generic segregates were described: *Dictyospermum* Wight and *Dichoespermum* Wight (Wight, 1853), *Lamprodithyros* Hasskarl (Hasskarl, 1863), *Rhopalephora* Hasskarl (Hasskarl, 1864b), *Piletocarpus* Hasskarl and *Prionostachys* Hasskarl (Hasskarl, 1866), *Bauschia* Seubert (Seubert, 1872), and *Amelina* C.B. Clarke (Clarke, 1874). Clarke (1881a) returned all of these generic segregates to *Aneilema* in his monograph of the Commelinaceae. However, Clarke (1874) also narrowed the concept of *Aneilema* by removing from it two of Brown's species, *A. crispatum* R. Brown and *A. macrophyllum* R. Brown, placing them in *Pollia*, following Bentham and Mueller (1878)

The concept of the genus remained unchanged until Brückner (1926) concluded that Clarke's *Aneilema* included two disparate genera: *Aneilema*, which he typified by *A. biflorum*, and *Phaeneilema* Brückner, which he described as new. Brückner (1930) subsequently recognized *Phaeneilema* as synonymous with *Murdannia* Royle and adopted the latter name. The fundamental distinction between *Aneilema* and *Murdannia* has been accepted by most authors with the notable exceptions of Hutchinson (1934, 1959), who later did adopt it (Hutchinson, 1973), and Woodson (1942). Woodson's *Aneilema* was even broader than that of Clarke (1881a) and included, in addition to *Murdannia*, neotropical taxa that had never been placed in the genus and were totally unrelated to it. Unfortunately, Woodson's nomenclature was adopted in a number of New World floristic works, and it has only slowly been abandoned.

The most recent change in the generic concept of *Aneilema* was that of Morton (1966), who transferred all of the southeastern Asiatic species to *Dictyospermum* or *Tricarpelema* J.K. Morton. I agree with Morton's circumscription of *Aneilema*, but I delimit the Asiatic genera that appear to be related to *Aneilema* differently (see "Generic Relationships of *Aneilema*," below).

In reviewing the typification of *Aneilema*, I came to the conclusion that the retypification of the genus by either *A. gramineum* R. Brown or *A. giganteum* R. Brown—now both treated as species of *Murdannia*—which could be justified on historic grounds, should be rejected because of the severe nomenclatural dislocation that would ensue and, strictly speaking, it is not necessary (Faden, 1978b). I accept *A. biflorum* as the lectotype of the genus, although it was selected in an arbitrary manner by Brückner (1926).

The history of the species of *Aneilema* sensu stricto is somewhat different from that of the genus. Except for a few that were described in genera such as *Commelina*, *Bauschia*, *Amelina*, *Lamprodithyros*, or *Floscopa*, nearly all species were first described in *Aneilema*. The first monograph of all of the known species was by Kunth (1843), who, as noted above, used a broad generic concept. Similarly, the next and last monograph to include all of the species was that of Clarke (1881a) whose subgenus *Dicarpellaria* is equivalent to *Aneilema* sensu stricto. All of the African species were monographed by Clarke (1901), who described many new ones. Since then many additional African species have been described, especially by Wildeman (1913, 1915), Chiovenda (1916, 1928, 1936), Brenan (1952, 1961, 1968), and Faden (1978a, 1984), and other species have been clarified, particularly by Morton (1966, 1967), Brenan (1952, 1961), and Faden (1984), but only regional floristic works have been published. A list of all specific names in *Aneilema* and their current status is given in Appendix II.

Generic Relationships of *Aneilema*

The generic relationships of *Aneilema* have been discussed in detail (Faden, 1975) and will be published separately. Therefore, only a summary will be included here. *Aneilema* appears to be most closely related to a group of three exclusively or mainly Asiatic genera that show the same one-sided stamen arrrangement, i.e., the three stamens (or three longer stamens) attached in front of the outer and usually lower petal and adjacent (inner) sepals. The three staminodes or smaller stamens, when present, are attached on the opposite side of the flower.

Among these genera, *Aneilema* is undoubtedly more closely related to *Rhopalephora* Hasskarl than to *Dictyospermum* Wight or *Tricarpelema* J.K. Morton. *Rhopalephora*, a genus of about three ill-defined species that range from India and Sri Lanka throughout southeast Asia to New Guinea and the Fiji

Islands plus one species in Madagascar (Faden, 1977), agrees with *Aneilema* (and differs from the other two genera) in having bivalved capsules that are bilocular or unequally trilocular (vs. trivalved and equally trilocular), perfoliate (vs. non-perfoliate) bracteoles, and clawed (vs. non-clawed) petals. In fact, *Rhopalephora* is so similar to *Aneilema* that it must be defined by a combination of characters, none of which is unique to it (except for the basic chromosome number $x = 29$).

Dictyospermum (*Dictyospermum* section *Dictyospermum* sensu Faden, 1975) consists of four to five species that are distributed from southern India and Sri Lanka to New Guinea. In addition to the characters cited above, it differs from *Aneilema* by its equal petals, absence of staminodes, and strictly one-seeded capsule locules that contain coarsely reticulate seeds.

Tricarpelema (*Dictyospermum* section *Tricarpelema* sensu Faden, 1975), the least understood of these genera, contains six species that range from the foothills of the Himalayas in India to the Philippines and Borneo, and possibly a seventh species in western Africa (Cameroon and Gabon). It differs from *Aneilema* by its shorter, upper androecium-members sometimes polliniferous and in its lack of hook-hairs, plus the features mentioned above.

Another species in this alliance, described as *Floscopa yunnanensis* Hong (Hong, 1974) from Yunnan Province, China, but clearly not belonging to that genus, is of uncertain generic position. It seems closer to *Aneilema* and *Rhopalephora* than to *Dictyospermum* or *Tricarpelema*, but it cannot be comfortably accommodated in any of these genera. It is still inadequately known, having been collected only once. A detailed account of its morphology and possible relationships is given in Faden (1975).

Two species that must either be placed in *Aneilema* or else segregated as monotypic, closely related genera are *A. calandrinoides* F. Mueller of Australia and *A. brasiliense* C.B. Clarke of Brazil and Venezuela. They are discussed at the end of the taxonomic treatment under "Species of Uncertain Generic Position."

The genus *Pollia* may be the sister group for the entire alliance of genera and species discussed above. Although it includes species with the same one-sided arrangement of stamens and staminodes as in *Aneilema* and the other genera, *Pollia* also contains other species that have six equal, fertile stamens. The one-sided stamen and staminode arrangement has evolved within *Pollia*, and thus the genus is convergent rather than synapomorphic with the *Aneilema* alliance genera and species with regard to this character.

The genus *Murdannia* must be mentioned because of the historic placement of its species in *Aneilema* (see Faden, 1978a). Its alternating stamen and staminode arrangement, however, is clearly a separate, derived state from the androecial structure in *Aneilema* and related genera. *Murdannia* also exhibits further unusual and apparently derived characters, such as three-lobed antherodes (first noted by Brenan, 1952) (Figure 43) and a continuous adaxial hypodermis (Tomlinson, 1966), that are not present in the other genera and that indicate an early separation from *Pollia* and the taxa of the *Aneilema* alliance.

Aneilema has also been considered closely related to

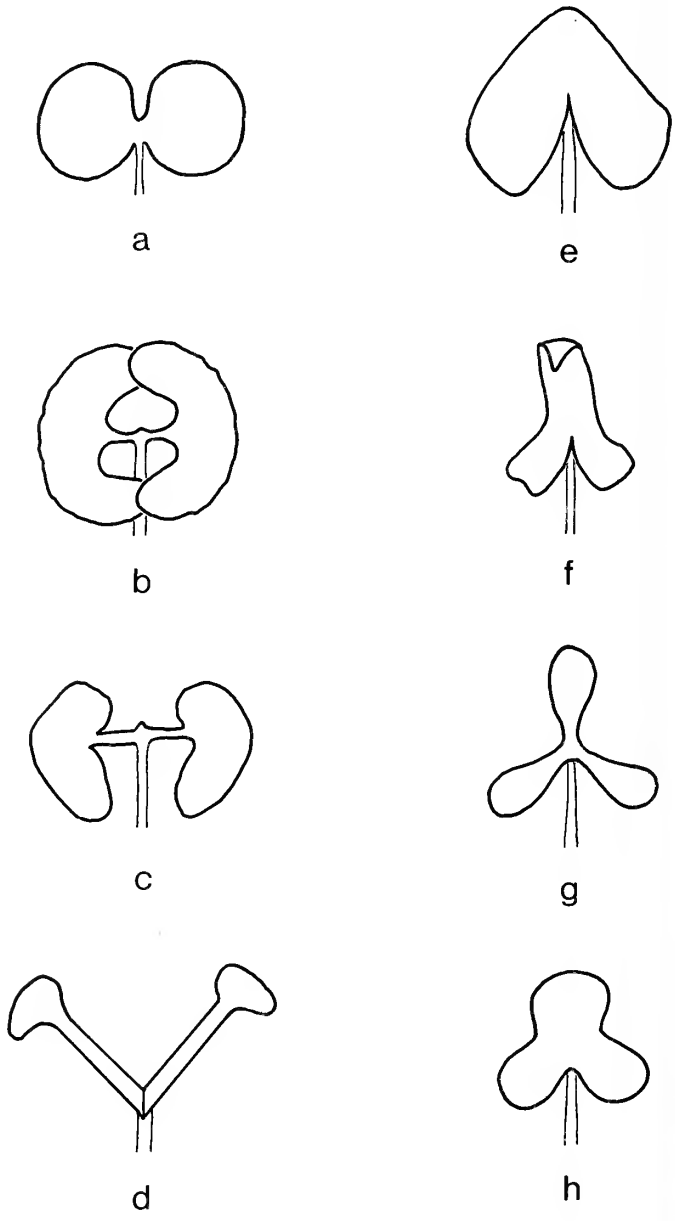


FIGURE 43.—Antherodes of *Aneilema* and *Murdannia*. *Aneilema* (*a-d*): *a*, *A. petersii* (Hasskarl) C.B. Clarke subsp. *pallidiflorum* Faden, lateral antherode (from *Faden et al. 69/1068*); *b*, *A. umbrosum* (Vahl) Kunth subsp. *ovato-oblongum* (P. de Beauvois) J.K. Morton, lateral antherode (from *Lye & Katende 6235*); *c*, *A. rendlei* C.B. Clarke, medial antherode (from *Faden et al. 69/322*); *d*, *A. hockii* De Wildeman, lateral antherode (from *Faden et al. 72/234*). *Murdannia* (*e-h*): *e*, *M. japonica* (Thunb.) Faden (after Clark, 1904, as *Aneilema lineolatum* (Blume) Kunth); *f*, *M. clarkeana* Brenan (from *Faden & Evans 69/304*); *g*, *M. simplex* (Vahl) Brenan (from *Faden et al. 74/64*); *h*, *M. zeylanica* (C.B. Clarke) Brückner (from *Davidse s.n.*). (Not to scale.)

Commelina by Rohweder (1969) on the basis of 13 shared characters. I have rejected this argument for three reasons: (1) some of the characters used, such as the minor anatomical ones, are of unknown phylogenetic significance, i.e., the primitive and derived conditions are unclear; (2) some characters used, e.g., presence of a terminal inflorescence, are plesiomorphic and are therefore not indicative of an evolutionary relationship; and (3) some similarities, particularly those of the androecium, may be due to convergence (Faden, 1975).

Finally, it must be stressed that that a cladistic analysis of all of the genera that comprise the tribe *Commelineae* (sensu Faden, 1985), to which *Aneilema* and all of the above-mentioned genera, as well as others, belong, is urgently needed. Until that is undertaken, the results of this present analysis of the relationships among some of these genera must be considered preliminary.

Citations of *Aneilema*

Aneilema R. Brown, Prod. Fl. Novae-Hollandiae, 270, 1810, p.p.—P. de Beauvois, Fl. Owar., 2:56, 1818, p.p.—Bentham in Hooker and Bentham, Fl. Nigrit., 546, 1849, p.p.—Bentham and Mueller, Fl. Austral., 7:85, 1878, p.p.—Clarke, J. Bot., 19:199, 1881, p.p.—Clarke in DC, Monogr. Phan., 3:195, 1881, p.p.—Bentham and Hooker, Gen. Pl., 3:849, 1883, p.p.—Bailey, Synopsis Queensland Fl., 556, 1883, p.p.—Schumann in Engler, Pflanzenwelt Ost-Afrikas C, 135, 1895, p.p.—Durand and Schinz, Conspect. Fl. Africae, 5:429, 1895, p.p.—Durand and Schinz, Etud. Fl. Congo, 1:270, 1896, p.p.—Clarke in Thiselton-Dyer, Fl. Capensis 7, 1:12, 1897, p.p.—Durand and De Wildeman, Bull. Soc. Roy. Bot. Belgique, 36:87, 1897, p.p.; 37:128, 1898, p.p.—De Wildeman and Durand, Ann. Mus. Congo Bot., Sér. 2, 1:62, 1899-1900, p.p.—Clarke in Thiselton-Dyer, Fl. Trop. Africa, 8:62, 1901, p.p.—Bailey, Queensland Fl., 5:652, 1902, p.p.—Durand and Durand, Syll. Fl. Congo., 579, 1909, p.p.—Bailey, Cat. Queensland Pl., 561, 1913, p.p.—Chevalier, Etudes Afr. Cent. Franc., 1:328, 1913, p.p.—Thonner, Fl. Pl. Africa, 122, 1915, p.p.—Chiovenda, Result. Scient. Miss. Stefanini-Paoli Somalia Italiana, 1:167, 1916.—Ewart and Davies, Fl. Northern Terr., 69, 1917, p.p.—Chevalier, Explor. Bot. Afr. Occident. Franc., 1:666, 1920, p.p.—Brückner, Bot. Jahrb. Syst., Beibl., 137:62, 1926, p.p. maj.—Chiovenda, Fl. Somala, 1:316, 1929.—Brückner in Engler, Naturlich. Pflanzenfam., ed. 2, 15a:174, 1930, p.p. maj.—Hutchinson, Fam. Fl. Pl., 2:55, 1934, p.p.—Hutchinson and Dalziel, Fl. W. Trop. Africa 2, 2:312, 1936, p.p.—Perrier de la Bâthie, Notul. Syst. (Paris), 5:193, 1936, p.p. min.—Perrier de la Bâthie, Fl. Madagascar, 23, 1938, p.p. min.—Chiovenda in Zavatti, Miss. Biol. Paese Borana, 4:304, 1939.—Pichon, Notul. Syst. (Paris), 12:238, 1946, p.p. maj.—Täckholm and Drar, Fl. Egypt, 2:433, 1950.—Chiovenda, Webbia, 8:38, 1951.—Brenan, Kew Bull., 7:180, 1952, p.p. maj.—Robyns and Tournay, Fl. Spermat. Parc Natl. Albert, 3:326, 1955.—Andrews, Fl. Pl. Sudan, 3:238, 1956.—Troupin, Fl. Spermat. Parc Natl. Garamba, 1:158, 1956.—Hutchinson, Fam. Fl. Pl., ed. 2, 2:565, 1959, p.p.—Panigrahi and Kammathy, Proc. Natl. Acad. Sci. India, Sect. B, 33:491, 1963, speciebus excl.—Brenan, Kew Bull., 19:63, 1964, p.p. maj.—Aristeguieta, Bol. Acad. Cien. Fís. Matemát. Nat. Caracas, 25:134, 1965.—Compton, J. S. Afr. Bot., uppl., 6:33, 1966.—Morton, J. Linn. Soc., Bot., 59:431, 1966.—Schreiber in Merxmüller, Prod. Fl. Südwestafrika, 157:2, 1967.—Morton, J. Linn. Soc., Bot., 60:167, 1967.—Brenan, Kew Bull., 22:387, 1968.—Brenan in Hepper, Fl. W. Trop. Africa, ed. 2, 3, 1:29, 1968.—Rohweder, Ber. Schweiz. Bot. Ges., 79:216, 1969.—Cufodontis, Bull. Jard. Bot. Natl. Belgique, 41, suppl., 1516, 1971.—Lebrun, Andru, Gaston, and Mosnier, Inst. Elevage Med. Vétérin. Pays Trop. Etude Bot., 1:185, 1972.—Ross, Fl. Natal, 117, 1972.—Faden in Agnew, Upland Kenya Wild Fl., 664, 1974.—Faden, Bothalia, 12:565, 1978.—Faden, Taxon, 27:289, 1978.—Faden, Fl. Pl. Africa, 43:1785, 1979.—Faden and Suda, Bot. J. Linn. Soc., 81:301, 1980.—Faden in Morley and Toelken, Flowering Plants in Australia, 368, 1983.—Faden, Bothalia, 14:553, 1983.—Faden, Bothalia, 14:997, 1983.—Faden, Bothalia, 15:89, 1984.—Obermeyer and Faden in Leistner, Fl. Southern Africa, 4(2):23, 1985.

Synonymy of *Aneilema*

Commelina auct., p.p. [non L. (1753)].

Anilema Kunth, Enum. Pl., 4:64, 1843 [orth. var. of *Aneilema* R. Brown].

Lamprodithyros Hasskarl, Flora, 46:388, 1863; in Peters, Naturwiss. Reise Mossambique, Bot., 529, 1864. [Lectotype: *L. petersii* Hasskarl = *Aneilema petersii* (Hasskarl) C.B. Clarke.]

Perosanthera Fenzl, Sitzungsb. Akad. Wien, 50:353, 1864 [nom. nud. in comb.]

Bauschia Seubert in Warming, Vidensk. Meddel. Kjöb., 1872:123, 1872. [Type: *B. bracteolata* (Martius) Seubert = *Aneilema umbrosum* (Vahl) Kunth.]

Amelina C.B. Clarke, Commel. et Cyrt. Beng., 38, tab. 26, 1874. [Type: *A. wallichii* C.B. Clarke = *Aneilema aequinoctiale* (P. de Beauvois) G. Don.]

Aneilema subgenus *Dicarpellaria* C.B. Clarke in De Candolle, Monogr. Phan., 3:196, 1881.

Ballya Brenan, Kew Bull., 19:63, 1964. [Type: *B. zebrina* (Chiovenda) Brenan = *Aneilema zebrinum* Chiovenda.]

Description of *Aneilema*

Perennial and annual herbs of various habits. Roots fibrous or tuberous. Leaves spirally arranged or distichous, sheaths entire, usually ciliate at the apex, laminae petiolate or sessile, usually herbaceous (rarely succulent). Uppermost leaf (inflorescence bract) on the flowering shoot often very reduced.

Inflorescences thyrses, terminal, terminal and axillary, or rarely, all axillary, consisting of a central axis bearing individual cincinni, rarely reduced to a single cincinnus. Cincinni always subtended by persistent bracts, which are often glandular near the apex. Bracteoles 2-ranked on the cincinnus,

frequently cup-shaped, perfoliate, usually glandular near the apex, persistent.

Flowers pedicellate, perfect, perfect, and staminate, or, rarely, perfect, staminate, and pistillate, all types produced in the same inflorescence. Sepals 3, free, sepaloid, persistent, convexo-concave, usually hooded apically, particularly the medial one, predominantly green, usually glandular near the apex, glabrous or puberulous. Petals 3, free, petaloid, deliquescent, subequal and concolorous or, more commonly, the medial one much reduced (rarely enlarged) and discolorous; paired petals usually held upwards, always unguiculate, white to lilac or lavender, or yellow to orange, rarely red, claws glabrous, rarely puberulous; medial petal usually held downwards, cuneate at base, rarely unguiculate, commonly dull colored and inconspicuous, rarely puberulous basally. Staminodes 3(-2), opposite the medial sepal and paired petals, equal or, more commonly, the medial (antesepalous) one reduced (sometimes vestigial or absent), when present its antherode often different in size and/or shape from those of the lateral staminodes; antherodes bilobed (rarely unlobed), the lobes stipitate or sessile, filaments always glabrous. Fertile stamens 3, opposite the paired sepals and medial petal, equal or, more commonly, the medial (antepetalous) one much shorter than the lateral (antesepalous) ones, all filaments glabrous, or the laterals sparsely to densely bearded with uniseriate, non-moniliform hairs; anthers basifixed, dorsifixed or versatile, dehiscence longitudinal, usually introrse, rarely latrorse or extrorse; anther of the medial stamen usually different in size and/or shape from those of the lateral stamens, its pollen often also different in color and sometimes inviable. Ovary stipitate or sessile, bi- or trilocular, glabrous or, more commonly, puberulous with glandular hairs (occasionally mixed with few to many hook-hairs), dorsal locule not developed or with one (rarely more) ovule(s), ventral locules each with 1–6 uniseriate ovules; style simple, stigma capitate or not enlarged.

Fruit capsular, usually dehiscent, rarely ± indehiscent, bi- or trilocular, bi- or (very rarely) trivalved, usually gray to brown, generally lustrous, glabrous, or puberulous, valves persistent or the dorsal one deciduous, dorsal locule (when present) empty or with one (rarely more) seed(s), ventral locules each with up to 6 uniseriate seeds. Seeds with a linear hilum and lateral embryotega, testa various, often with farinose granules.

TYPE SPECIES.—*Aneilema biflorum* R. Brown (see Faden, 1978b).

DIVISION OF *Aneilema* INTO SECTIONS

The first formal division of *Aneilema* into sections was proposed by Clarke (1881a:196), who used the following scheme:

Subgenus I. Tricarpellaria. Capsule subequally 3-locular, 3-valved.
Section I. Euaneilema. Ovary with locules 2-many-ovulate; seeds 1-seriate.
Section II. Dichaespermum. Ovary with locules many-ovulate; seeds 2-seriate.
Section III. Dictyospermum. Ovary with locules 1-ovulate.
Subgenus II. Dicarpellaria. Capsule 2-locular, 2-valved (a third smaller locule rarely added).
Section IV. Amelina. Capsule with apex truncate, 2-horned, with locules 3–5-seeded.
Section V. Lamprodithyros. Capsule with apex obtuse rounded, with locules 2-several-seeded (1-seeded in *A. siliculosum*).

Clarke's subgenus *Tricarpellaria* does not include any species of *Aneilema* in the circumscription of the genus used here. Its species are assignable to *Murdannia* Royle, *Dictyospermum* Wight, *Tricarpelema* J.K. Morton, and *Anthericopsis* Engler. Subgenus *Dicarpellaria* equals *Aneilema* in the present sense. Clarke's sections *Amelina* and *Lamprodithyros* are the earliest published names for sections of *Aneilema* in the sense used here.

Clarke's divisions were accepted by Bentham and Hooker (1883) as "apparently well limited although not always natural." They were also used but evidently not understood by Schumann (1895), who placed two of his three just described species of *Aneilema* in section *Euaneilema* instead of section *Lamprodithyros*, where they should have been put according to Clarke's characters.

Clarke (1901:62–63) slightly revised subgenus *Dicarpellaria* by dividing it into three instead of two sections as follows:

Amelina: Panicles terminal. Capsule truncate, with 2 acute corners.
Lamprodithyros: Panicles terminal. Capsule ellipsoid without angles at the top.
Pseudo-axillares: Panicles appearing irregularly scattered, all terminal, but not rarely on remote short axillary branches.

Morton (1966) followed Clarke (1881a) in using two sections, *Amelina* and *Lamprodithyros*, defining them in the same way. He did not accept section *Pseudo-axillares* of Clarke (1901), however, stating that its species "fall naturally into the section *Lamprodithyros*."

I have found that the schemes proposed thus far for dividing *Aneilema* into sections are artifical and totally inadequate for expressing the natural relationships among the species in the genus. The single character used by Clarke (1881) and Morton (1966)—shape of the capsule apex—would in some cases separate closely related species, e.g., *A. hockii* and *A. longirrhizum*, and in others associate only distantly related ones, e.g., *A. pedunculosum* and *A. acuminatum*. My detailed investigation of characters of potential use in defining sections has revealed that, in general, floral attributes are more indicative of natural relationships in *Aneilema* than are capsular characters. However, capsule, seed, inflorescence, and, to a lesser extent, vegetative characters have also been found to be useful in some cases. These characters have been employed as much as possible because of the generally poor preservation of floral parts in dried specimens.

In the following scheme, section *Aneilema* is recognized for the first time, Clarke's section *Amelina* has been redefined and somewhat expanded, and his section *Lamprodithyros* has been greatly restricted in scope but still includes his section *Pseudo-axillares*. In addition, four new sections have been

described.

The seven sections proposed in this scheme are each held together by numerous morphological characters. Moreover, each section has a distinctive geographic distribution and generally only one or two basic chromosome numbers. Most sections also have characteristic patterns of floral hair types on the different floral whorls. No subsections or series have been recognized, although within some sections there are species groups that might warrant such formal taxonomic recognition on the basis of future investigations.

Key to the Sections of *Aneilema*

1. Medial petal equal to or larger than a lateral petal, usually concolorous with it; stamen filaments glabrous; all 3 anthers well developed; Australo-Oceanic, African, and Arabian Peninsular species.
   2. Ovaries and capsules glabrous; medial petal not boat-, slipper-, or cup-shaped; filaments free; seeds with a rugose testa, lacking farinose granules; Australo-Oceanic and Madagascan species . . . . . 1. Section ***Aneilema***
   2. Ovaries and capsules puberulous; medial petal boat-, slipper-, or cup-shaped; stamen filaments fused basally; seeds with a scrobiculate to reticulate testa, usually farinose in the depressions; continental African and Arabian Peninsular species . . . . . 5. Section ***Lamprodithyros***
1. Medial petal usually much smaller than a lateral petal and differently colored from it (if subequal, then lateral stamen filaments bearded and medial anther reduced); stamen filaments glabrous or bearded; anther development various; African and American species.
   3. Capsules glabrous; medial anther large, elliptic to ovate, with a strongly convex, maroon-spotted connective; lateral stamen filaments of staminate flower and style of perfect flower J-shaped; filaments glabrous; stigma not enlarged . . . . . 3. Section ***Rendlei,*** new section
   3. Capsules puberulous or glabrous; medial anther various, but not as above; curvature of lateral stamen filaments and style various, but not J-shaped, filaments bearded or glabrous; stigma usually distinctly capitate (not capitate in section *Somaliensia*).
      4. Inflorescences lax with cincinni mostly subopposite or subverticillate (mostly alternate in *A. longirrhizum*); flowers usually medium to large, 12–40 mm wide (if less, then paired petals yellow to orange); lateral stamen filaments straight or undulate, not geniculate . . . . . 2. Section ***Amelina***
      4. Inflorescences dense to moderately lax (rarely lax) with mostly alternate cincinni; flowers small to medium, 4–15(–20) mm wide; lateral stamen filaments S-shaped, ± geniculate.
         5. Stamen filaments glabrous; tuberous-rooted perennials generally of dry bushland (habit and roots of *A. grandibracteolatum* unknown); flowering shoots often disarticulating at the nodes at the end of the growing season . . . . . 4. Section ***Somaliensia,*** new section
         5. Stamen filaments bearded; perennials or annuals, fibrous or tuberous-rooted, generally of grassland or forest, rarely of bushland; flowering shoots not disarticulating at the nodes.
            6. Lateral stamens usually sparsely and inconspicuously bearded; bracteoles cup-shaped, generally perfoliate, lacking linear apices; cincinnus axes usually elongate (except in *A. paludosum* and *A. mortonii*); tuberous roots sometimes present . . . . . 6. Section ***Brevibarbata,*** new section
            6. Lateral stamens densely and conspicuously bearded; bracteoles neither cup-shaped nor perfoliate, often with linear, gland-tipped apices; cincinnus axes usually not elongate, rarely somewhat elongate; tuberous roots absent . . . . . 7. Section ***Pedunculosa,*** new section

Section 1: *Aneilema*

Perennial or annual herbs with fibrous or tuberous roots. Leaves spirally arranged, with sheaths usually lacking long cilia at the apex.

Inflorescences thyrses, terminal on the main or short lateral shoots, lax to moderately lax. Inflorescence axes puberulous with hook-hairs of uniform length. Bracteoles herbaceous, cup-shaped, perfoliate.

Flowers all perfect or perfect and staminate. Fruiting pedicels erect, laterally spreading, or sharply decurved. Petals subequal, concolorous, white to blue-violet, glabrous, medial petal neither cup-shaped nor retaining the lateral stamens. Filaments free. Staminodes equal or subequal, antherodes unlobed or bilobed, yellow or white to violet. Stamens equal or the medial shorter than the laterals and its anther of a different form, filaments straight to very gently S-shaped, glabrous. Ovary sessile, glabrous, dorsal locule not developed or 1-~5-ovulate, ventral locules each 1-~5-ovulate; stigma capitate.

Capsules sessile, dehiscent, bi- or trilocular, bi- or trivalved, lustrous, glabrous, apex acute or rounded to truncate or emarginate, valves persistent and spreading to ~180° or dorsal valve deciduous, dorsal locule (when present) 1-~5-seeded, ventral locules each 1-~5-seeded, cells of the capsule wall transversely elongate. Seeds with hilum short, testa rugose-tuberculate, lacking farinose granules.

TYPE SPECIES.—*Aneilema biflorum* R. Brown (see Faden, 1978b).

BASIC CHROMOSOME NUMBER.—$x = 16$.

DISTRIBUTION.—Ternate Island (Indonesia) to the Solomon Islands, S to Northern Territory, N and E Queensland, E New South Wales, Australia, New Caledonia and the New Hebrides; also in Madagascar.

Key to the Species of Section *Aneilema*

1. Leaves sessile; roots tuberous; capsules with ventral locules 1-seeded . . . . . ***A. siliculosum***
1. Leaves petiolate; roots fibrous; capsules with ventral locules 2-several seeded.
   2. Sepals and pedicels puberulous; ventral locules of capsule 2-seeded.
      3. Plants not rhizomatous; inflorescences 10–25 cm long, with (4–)8–18 cincinni; dorsal capsule valve persistent; Madagascar . . . . . ***A. aparine***
      3. Plants rhizomatous; inflorescences 2.5–6 cm long, with (1–)2–6 cincinni; dorsal capsule valve deciduous; Australia . . . . . ***A. sclerocarpum***
   2. Sepals and pedicels glabrous; ventral locules of capsule 2–5-seeded.
      4. Inflorescences consisting of 1–4 cincinni, borne on short lateral shoots; fruiting pedicels deflexed.
         5. Leaves linear to linear-lanceolate; flowers 1.2–2.0 cm wide; anthers linear to linear-oblong; pollen white . . . . . ***A. neocaledonicum***
         5. Leaves lanceolate; flowers less than 1 cm wide; anthers ovate to ovate-elliptic; pollen yellow . . . . . ***A. biflorum***
      4. Inflorescences consisting of 4–many cincinni, terminal on the main and major lateral shoots; fruiting pedicels horizontal to erect . . . . . ***A. acuminatum*** (including *A. papuanum*)

SPECIES CITATIONS AND DISTRIBUTIONS

Aneilema acuminatum R. Brown, Prod. Fl. Novae-Hollandiae, 270, 1810 [ternate to the Solomon Islands S to Australia (Queensland, NSW) (Plate 1*a*,*b*)].

Aneilema aparine H. Perrier de la Bâthie, Notul. Syst. (Paris), 5:196, 1936 [Madagascar].

Aneilema biflorum R. Brown, Prod. Fl. Novae-Hollandiae, 270, 1810 [Australia (Queensland, NSW)].

Aneilema neocaledonicum Schlechter, Bot. Jahrb. Syst., 39:28, 1906 [New Caledonia and the New Hebrides (Plate 1*c*)].

Aneilema sclerocarpum F. Mueller, Frag., 8:61, 1873 [Australia (Queensland)].

Aneilema siliculosum R. Brown, Prod. Fl. Novae-Hollandiae, 270, 1810 [Australia (N Territory, N Queensland)].

DISCUSSION

The diversity in morphology and wide geographic distribution of this section suggest an old radiation. The major taxonomic problem is the final disposition of *A. papuanum*, which is tentatively included within *A. acuminatum* herein. *Aneilema papuanum* is geographically almost completely discrete from typical *A. acuminatum* and thus merits at least subspecific rank, but further study is required to determine whether it should be accepted as a full species. The placement of the Madagascan *A. aparine* in section *Aneilema* is based on a congruence of many characters, including floral morphology

as determined by dissection of buds on a herbarium specimen.

Section 2: *Amelina* (C.B. Clarke) C.B. Clarke

Aneilema section *Amelina* (C.B. Clarke) C.B. Clarke in De Candolle, Monogr. Phan., 3:197, 1881; in Thiselton-Dyer, Fl. Trop. Africa, 8:62, 1901.—Morton, J. Linn. Soc., Bot., 59:439, 1966. [Lectotype: *Aneilema aequinoctiale* (P. de Beauvois) G. Don.]

Amelina C.B. Clarke, Commel. et Cyrt. Bengal., 39, tab. 26, 1874, pro gen. [type: *Amelina wallichii* C.B. Clarke (= *Aneilema aequinoctiale* (P. de Beauvois) G. Don).]

Perennial or rarely annual herbs with fibrous or tuberous roots. Leaves spirally arranged or distichous.

Inflorescences thyrses, terminal on the main shoots and occasionally on shorter lateral shoots, lax, with mostly subopposite or subverticillate (rarely mostly alternate) cincinni. Inflorescence axis and cincinnus peduncles and axes usually puberulous with hook-hairs of two sizes (rarely all glabrous). Cincinni elongate. Bracteoles usually herbaceous and cup-shaped, perfoliate (rarely membranous and not perfoliate).

Flowers mostly relatively large (10–40 mm wide), perfect and staminate (rarely pistillate, perfect, and staminate). Fruiting pedicels erect (rarely recurved 270°), persistent. Lateral sepals narrow, generally lanceolate to lanceolate-elliptic, commonly puberulous with hook-hairs of two sizes (rarely glabrous or with uniform hook-hairs). Paired petals lilac to lavender or yellow to orange, claws glabrous or puberulous. Medial petal reduced, usually inconspicuous, rarely concolorous with the paired petals. Filament bases usually free (rarely fused). Staminodes with yellow, bilobed antherodes; medial staminode very short, its lobes usually larger than those of the lateral staminodes (rarely all three staminodes short and their antherodes equal). Lateral staminodes with filaments straight to arcuate, sometimes strongly recurved near the apex. Lateral stamens with filaments straight or undulate, parallel or divergent, glabrous or bearded. Medial stamen with filament strongly ascending apically, anther very reduced or large and saddle- or shield-shaped, when large, commonly with a contrasting dark spot or bar on the yellow connective. Ovary sessile or stipitate, very sparsely to densely puberulous, usually glabrous on the lateral and middorsal sutures, dorsal locule not developed or 1-ovulate, ventral locules each 2–6-ovulate; style straight or undulate, sometimes strongly recurved apically, usually held ± in the floral midplane, stigma capitate.

Capsules sessile or stipitate, dehiscent, bivalved, bi- or trilocular, lustrous or dull, apex acute to rounded, truncate or emarginate, valves persistent and spreading up to 180°, or occasionally dorsal valve deciduous, dorsal locule (when present) 1-seeded or, by abortion, empty; ventral locules up to 6-seeded (rarely regularly empty by abortion), cells of the capsule wall isodiametric or transversely elongate. Seeds usually oblong to trapezoidal (occasionally ovate or elliptic), apical ventral generally rounded apically, basal ventral generally rounded to truncate basally, the apical and basal seeds therefore usually little differentiated in shape (rarely strongly differentiated), hilum commonly not in a groove (occasionally in a groove), often slightly extended onto apical and basal surfaces, testa smooth to alveolate, shallowly foveate, reticulate-foveate or scrobiculate, farinose granules present or absent.

BASIC CHROMOSOME NUMBERS.—x = 13, 15, and 16.

DISTRIBUTION.—Throughout the continental African range of the genus except for the extreme N and NE; better represented on the eastern side of the continent than in the west.

Key to the Species of Section *Amelina*

1. Inflorescence axis and cincinnus peduncles and axes glabrous; paired petals yellow-orange; stamen filaments glabrous; tuberous rooted perennials . . . . . ***A. johnstonii***
1. Inflorescence axis and cincinnus peduncles and axes puberulous; paired petal color, stamen filament pubescence and habit various, but not in the above combination.
   2. Bracteoles not perfoliate, membranous; capsule glabrous or subglabrous, apex acute; stamen filaments finely bearded in basal half . . . . . ***A. gillettii***
   2. Bracteoles perfoliate, herbaceous; capsule puberulous, apex rounded to truncate or emarginate; stamen filaments glabrous or bearded, if bearded, then not solely in basal half.
      3. Leaf margins smooth; paired petals pale lavender; fruiting pedicels recurved 270°; seeds 2 per ventral locule, densely covered with white farinose granules . . . . . ***A. longirrhizum***
      3. Leaf margins scabrid; petal color various; fruiting pedicels erect or spreading laterally; seeds 0–6 per ventral locule, lacking white farinose granules.
         4. Paired petals lilac or lavender; stamen filaments bearded; capsules strongly compressed laterally, rounded apically, dorsal locule with 1 very large, smooth seed ~6 mm long, ventral locules abortive, cells of the capsule wall isodiametric . . . . . ***A. plagiocapsa***

4. Paired petals lavender or yellow to orange; stamen filaments bearded or glabrous; capsules not laterally compressed, truncate to emarginate apically, dorsal locule not developed or with 1 seed less than 3 mm long, ventral locules 1–6-seeded, cells of the capsule wall isodiametric or transversely elongate.
   5. Paired petals lavender; stamen filaments glabrous; roots tuberous or fibrous; capsules with ventral locules 4–6-seeded (occasionally less by abortion), cells of the wall transversely elongate . . . . . ***A. hockii***
   5. Paired petals yellow to orange-yellow; stamen filaments bearded or glabrous; roots fibrous; capsules with ventral locules 1–3-seeded, cells of the wall isodiametric.
      6. Annuals with spirally arranged leaves; stamen filaments glabrous . . . . . ***A. ephemerum***
      6. Perennials with distichous leaves; stamen filaments bearded.
         7. Sheaths with whitish hairs at the apex; flowers ~18–30 mm wide; claws of the paired petals bearded; pollen orange; seeds 3 per ventral locule . . . . . ***A. aequinoctiale***
         7. Sheaths with orange or reddish orange hairs at the apex; flowers ~10–15 mm wide; claws of the paired petals glabrous; pollen white; seeds 1–2 per ventral locule . . . . . ***A. nyasense***

Species Citations and Distributions

Aneilema aequinoctiale (P. de Beauvois) G. Don in Loudon, Hort. Brit., 15, 1830 [basionym: *Commelina aequinoctialis* P. de Beauvois, Fl. Owar, 1:65, tab. 38, 1806; S Ethiopia to Guinea S to Angola, Zimbabwe, and South Africa (Natal, Cape, Transvaal) (Plate 1*i*)].

Aneilema ephemerum Faden, ined. [*Faden & Faden 74/794;* N Kenya].

Aneilema gillettii Brenan, Kew Bull., 15:212, 1961 [S Ethiopia and N Kenya (Plate 1*e,f*)].

Aneilema hockii De Wildeman, Feddes Repert. Spec. Nov. Regni Veg., 12:290, 1913 [S Ethiopia S to Mozambique, South Africa (Transvaal), Botswana, and Namibia (Plate 1*g,h,l*)].

Aneilema johnstonii K. Schumann in Engler, Pflanzenwelt Ost-Afrikas C, 135, 1895 [S Ethiopia S to Mozambique, Zimbabwe and Botswana (Plate 1*d*)].

Aneilema longirrhizum Faden, Bothalia, 12(3):565, 1978 [South Africa (Transvaal) (Plate 1*k*)].

Aneilema nyasense C.B. Clarke in Thiselton-Dyer, Fl. Trop. Africa, 8:66, 1901 [W Zaire to Uganda S to Burundi, Malawi, and Mozambique (Plate 1*j*)].

Aneilema plagiocapsa K. Schumann in Warburg, Kunene-Sambesi-Exped., 184, 1903 [Zambia, S Zaire, and Angola].

Discussion

The species of section *Amelina* are very diverse, and their relationships to one another are often difficult to ascertain. This variability suggests that either the section is not monophyletic or, more likely, I believe, the extant species represent endpoints of an old radiation. This section is the only one that includes some species with glabrous lateral stamen filaments and others with bearded filaments. The occurrence of three basic chromosome numbers in section *Amelina* is shared only with section *Brevibarbata*, which has far more species. A number of unique characters for the genus occur in one or two species of section *Amelina*, e.g., paired petals claws puberulous (*A. aequinoctiale* and *A. ephemerum*). Indeed, nearly every species of the section has at least one attribute that is unique for *Aneilema*, e.g., stamen filaments bearded only in the basal half (*A. gillettii*); stamen filaments with branched hairs (*A. nyasense*); pollen dimorphic (*A. hockii*); capsules strongly compressed laterally with only the single dorsal locule seed developing (*A. plagiocapsa*). Many other characters present in section *Amelina* are uncommon in the genus as a whole, e.g., yellow petals, pistillate flowers, scented flowers, basally fused stamen filaments, hook-hairs on the stamen filaments, and isodiametric capsule wall cells.

Section *Amelina* is the most widespread section within Africa. This is due in large measure to the broad ranges of two species, *A. aequinoctiale* in forests throughout tropical Africa, and *A. hockii* in non-forest habitats in eastern and southern Africa.

Section 3: *Rendlei* Faden, new section

Staminodium medium erectum. Staminodia lateralia versus apicem valde recurvata. Stamina lateralia florum staminatorum filamentis prope basin valde deflexis, saepe formis litterae J, approximatis, parallelis, glabris. Stamen medium connectivo antherae valde convexo maculis sanguineis ornato. Ovarium glandulifero-microtrichomatibus sparsis, appressis praeditum, aliter glabrum. Stylus forma litterae J. Capsulae glabrae.

Type Species.—*Aneilema rendlei* C.B. Clarke.

Perennial or rarely annual herbs with fibrous or tuberous roots. Leaves spirally arranged.

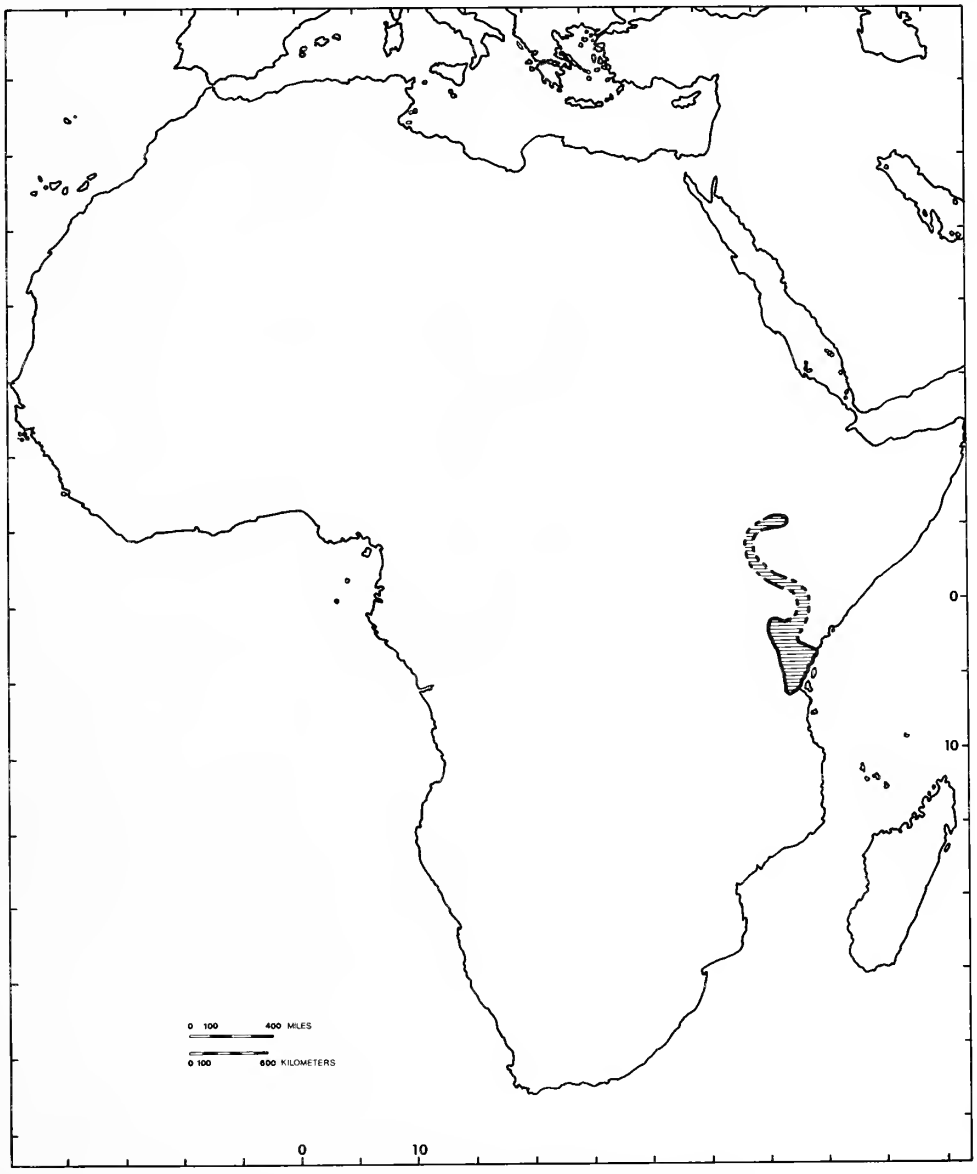
Inflorescences terminal (and occasionally axillary) thyrses with predominantly alternate cincinni. Inflorescence axis and cincinnus peduncles and axes glabrous or puberulous, uniseriate hairs absent. Bracteoles herbaceous, cup-shaped, perfoliate, prominently glandular near the apex, margin thickened (glandular?) towards the fused edge.

Flowers perfect and staminate. Fruiting pedicels usually erect, occasionally spreading laterally or decurved. Sepals prominently glandular, the gland of the medial sepal inconspicuously bilobed, those of the lateral sepals usually unlobed. Petals glabrous, the medial reduced, inconspicuous. Filament bases free. Medial staminode short, erect, antherode bilobed with lobes stipitate, generally reniform, often spotted with maroon adaxially, always larger than the lobes of the lateral staminodes, connective elongate. Lateral staminodes with filaments thickened basally, strongly deflexed, then strongly recurved towards the apex, antherodes bilobed with stipitate lobes. Lateral stamens dimorphic in perfect and staminate flowers, filaments J-, U-, or S-shaped, parallel in the staminate flowers, glabrous, anthers lanceolate to elliptic, pollen different in color from that of the medial stamen. Medial stamen with anther elliptic to ovate, connective very convex and maroon-spotted. Ovary sessile, oblong-elliptic, glabrous except for sparse, appressed, glandular microhairs mainly or exclusively on the lateral sutures and ventral surface, dorsal locule usually not developed, occasionally with an ovule, ventral locules each 2–6-ovulate; style J-shaped, held in the floral midplane, sharply deflexed at the base, stigma small.

Capsules sessile, oblong to oblong-elliptic, dehiscent, bivalved, usually bilocular, lustrous, glabrous, valves persistent, dorsal locule (when present) empty or 1-seeded, ventral locules each 2–5-seeded, cells of the wall transversely elongate, in regular files. Seeds trapezoidal, the apical rounded apically, the basal angular basally, hilum raised within a groove, testa scrobiculate, white-farinose in all the depressions and around the embryotega and hilum.

BASIC CHROMOSOME NUMBER.—$x = 16$.

DISTRIBUTION.—SW Ethiopia S to NE Tanzania (Map 4).



MAP 4.—Distribution of *Aneilema* section *Rendlei*, new section.

Key to the Species of Section *Rendlei*

1. Plants not rhizomatous; roots fibrous; leaves petiolate; inflorescence axis glabrous; flowers lilac to lavender.
   2. Shoots decumbent; fruiting pedicels to 8 mm long; capsules 3–6 mm long; seeds 1.3–1.6 mm wide.
      3. Cincinni 1–13 per inflorescence; leaves to 10 cm long; capsules stramineous, locules 2–3-seeded . . . . . 1. ***A. taylorii***
      3. Cincinni 14–20 per inflorescence; leaves to 16 cm long; capsules chocolate brown, locules 4-seeded . . . . . 2. ***A. usambarense,*** new species
   2. Shoots mostly erect or ascending; fruiting pedicels to 6.5 mm long; capsules 6–10 mm long; seeds 1.5–2 mm wide . . . . . 3. ***A. rendlei***
1. Plants rhizomatous; roots tuberous; leaves sessile; inflorescence axis puberulous; flowers white or nearly so . . . . . 4. ***A. brenanianum,*** new species

Discussion

Section *Rendlei* is very natural and homogeneous. The most distinctive features are the moderately to strongly dimorphic lateral stamen filaments in perfect and staminate flowers; strongly convex, maroon-spotted medial anther connective; and lack of hairs (other than inconspicuous glandular microhairs) on the ovaries. The only taxonomic problems are the possible division of *A. taylorii* into infraspecific taxa and the final determination of the status of the plant described below as *A. usambarense*. Resolution of these problems would require obtaining living material of these plants.

1. *Aneilema taylorii* C.B. Clarke

Aneilema taylorii C.B. Clarke ["Taylori"] in Thiselton-Dyer, Fl. Trop. Africa, 8:79, 1901 [type: Kenya (East Africa on label), Rabai Hills, Mombasa (Mombaz. on label), Fimbine? (probably = Fumbini on Kilifi Creek), Jul–Nov 1885, *W. E. Taylor s.n.* (BM)].

Aneilema rendlei Brenan, Kew Bull., 7:196, 1952, p.p. [non C.B. Clarke (1901)].

Aneilema sp. nov. aff. *A. umbrosum* (Vahl) Kunth, Morton, J. Linn. Soc., Bot., 59:464, 1966 [in adnot].

Perennial or annual herbs (habit type IA, Figure 1). Roots fibrous. Shoots decumbent, much branched, flowering shoots ascending, 15–30(–60) cm tall. Internodes 2–8(–9.5) cm long, puberulous, occasionally sparsely pilose as well. Leaves spirally arranged, sheaths 0.5–1.3 cm long, puberulous and frequently sparsely pilose, ciliate at the apex, laminae petiolate, lanceolate to lanceolate-elliptic or ovate, 2–10 cm long, 0.7–3(–4.3) cm wide, apex acuminate to acute, base cuneate, margin sometimes undulate, scabrid, adaxial surface patently hirsute-puberulous, uniseriate hairs 1–2.3 mm long, abaxial surface patently pilose-puberulous, uniseriate hairs very variable in number, sometimes confined to the veins, always shorter than those of the adaxial surface; petioles to 1.5(–2) cm long, ciliate on the margins.

Inflorescences thyrses (Figure 44*i*), terminal and occasionally axillary from the uppermost leaves, lax to moderately lax, ovoid, 1.5–5.5(–7) cm long, 1.5–6(–12) cm wide, with (1–)2–10(–13) cincinni, alternate to subopposite, patent to ascending (rarely the lower somewhat declinate). Peduncles (1.5–)2–5.5(–7.5) cm long, green, puberulous, often glabrous apically. Inflorescence bract medial, herbaceous, or occasionally membranous, generally very reduced, occasionally foliaceous. Inflorescence axis glabrous, slightly zigzag. Cincinni to 5(–6.5) cm long and 17(–18)-flowered. Cincinnus bracts herbaceous to membranous, lowermost sometimes perfoliate, appressed to the cincinnus peduncles, lanceolate or lanceolate-elliptic to oblong or ovate, 1.5–3 mm long, glandular near the cucullate apex, glabrous. Cincinnus peduncles relatively uniform in length within the inflorescence, exceeding the cincinnus bracts, (2.5–)3.5–8 mm long, glabrous. Cincinnus axes glabrous. Bracteoles attached (1.2–)2–3.5(–4.5) mm apart, herbaceous, eccentrically cup-shaped, perfoliate, 1–1.5 mm long, 0.4–0.8 mm high, with a prominent gland near the apex, glabrous, margin slightly thickened (glandular?) near the fused edge.

Flowers perfect and staminate (Plate 1*m,n*), odorless, (7–)9–15 mm wide. Pedicels 3.5–5.5(–6.5) mm long in flower, to 8 mm long in fruit, straight or gently arcuate in flower, erect, spreading laterally or decurved in fruit (sometimes all curvature types within the same inflorescence), persistent, glabrous. Sepals with a subapical, moderately prominent gland, glabrous; medial sepal elliptic to lanceolate-elliptic or lanceolate-ovate, 2.5–3.7 mm long, 1.8–2.4 mm wide, gland unlobed or bilobed; lateral sepals elliptic to oblong-elliptic or ovate-elliptic, 2–3.4 mm long, 1.6–2 mm wide. Paired petals (5.2–)5.5–9.5 mm long, (3.7–)4–7 mm wide, limb ovate to ovate-elliptic or ovate-suborbicular, 4–6.5 mm long, lilac to lavender (RHS colors: 87D, *Magogo in EA14203, Faden & Faden 74/371* and *77/611;* 76B-C, *Faden & Faden 74/371* and *77/611*), apex rounded, claw 1.5–3.5 mm long, concolorous with limb, glabrous. Medial petal reflexed, ovate to ovate-elliptic, 3–5 mm long, 2.3–3.7 mm wide, greenish white, sometimes tinged with lilac, margins colorless. All filament bases free. Medial staminode filament 1–2 mm long, reddish pink or reddish purple, antherode bilobed, lobes stipitate, flat, reniform or sickle-shaped, (0.3–)0.6–1 mm long,

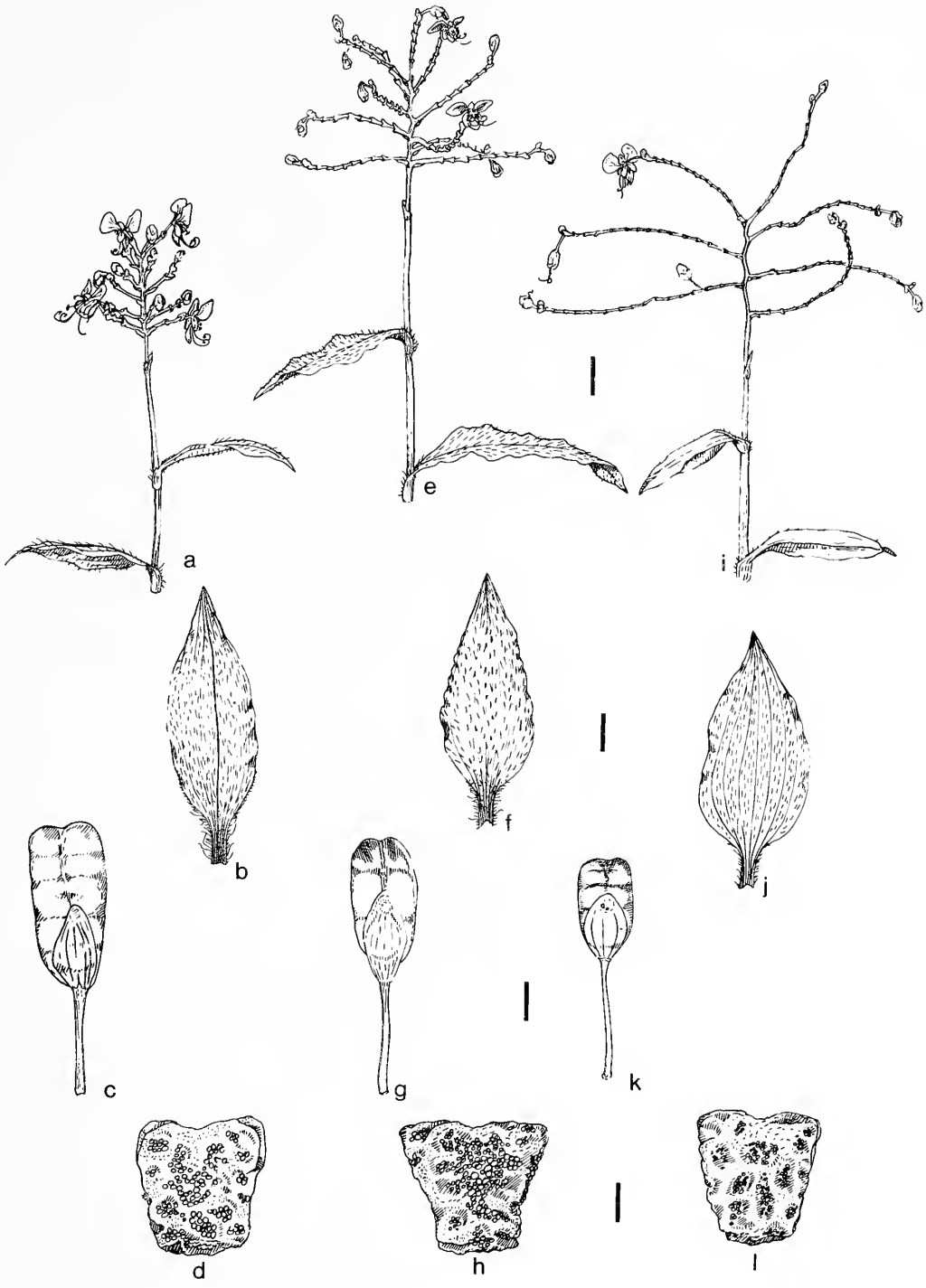


FIGURE 44.—Comparison of *Aneilema rendlei, A. taylorii,* and *A. rendlei* × *taylorii:* inflorescences, leaves, capsules, and seeds. *A. rendlei* C.B. Clarke (*a–d*): *a,* inflorescence; *b,* leaf; *c,* capsule; *d,* seed (from *Kabuye & Evans 163*). *A. rendlei* C.B. Clarke × *taylorii* C.B. Clarke (*e–h*): *e,* inflorescence; *f,* leaf; *g,* capsule; *h,* seed (from *Kabuye & Evans 163* (*rendlei*) × *Faden & Faden 74/371* (*taylorii*)). *A. taylorii* C.B. Clarke (*i–l*): *i,* inflorescence; *j,* leaf; *k,* capsule; *l,* seed (from *Faden & Faden 74/371*). (Bar = 10 mm for *a,b,e,f,i,j;* 2 mm for *c,g,k;* 0.5 mm for *d,h,l.*)

1.1–1.7 mm wide, yellow with small maroon or brown spots on the adaxial surface (these rarely absent), connective elongate. Lateral staminodes with filaments 3–6 mm long, arcuate-decurved then sharply recurved into a vertical position (Plate 5*n*), tapering from a thick base, reddish pink or purple, shading to yellow near the apex, antherodes bilobed, lobes stipitate, oblong, elliptic, elliptic-subreniform or C-shaped, (0.25–)0.4–0.6 mm long, yellow, sometimes with small maroon or brown spots on the adaxial surface, connective not at all or scarcely elongate. Lateral stamens moderately dimorphic (or sometimes not dimorphic?) in perfect and staminate flowers, shorter and more divergent in the former than in the latter (Figure 5*e,f,k,l*); filaments 4–10 mm long, decurved near the base, J- or S-shaped (Plate 5*n*), glabrous, anthers lanceolate to lanceolate-elliptic or elliptic, 0.9–1.4 mm long, 0.5–0.8 mm wide, connective whitish, creamy yellow or gray-green, pollen yellow or orange-yellow. Medial stamen with filament 3–6 mm long, anther broadly elliptic, 1–1.7 mm long, 0.7–0.9 mm wide (Figure 31*e,f*), usually held perpendicular to the ground, connective very convex, creamy white blotched with maroon, sometimes mostly maroon, pollen yellow or white or a mixture of yellow and white grains. Ovary not at all or scarcely stipitate, oblong-elliptic to ovate-oblong, 1–1.8 mm long, 0.8–1.1 mm wide, glabrous except for a few inconspicuous, appressed, glandular microhairs on the lateral sutures and sometimes also on the ventral surface (Figure 42*b*), apex truncate or rounded, dorsal locule represented by a low, middorsal ridge, empty, ventral locules each 2–3-ovulate; style 3.5–8.5 mm long, J-shaped (Plate 5*n*), sharply deflexed at base, held in floral midplane, ± uniform in thickness for most of its length, tapering near the apex, stigma small, whitish or yellowish, held below the stamens.

Capsules (Figure 44*k*) sessile, elliptic to broadly elliptic or oblong-elliptic, dehiscent, bivalved, bilocular, (2.8–)3–4.5 (–6) mm long, 2–3.2 mm wide, stramineous, lustrous, glabrous, apex emarginate to truncate, valves persistent, locules 2–3-seeded, cells of the capsule wall transversely elongate. Seeds (Figure 44*l*; Plate 5*a*) trapezoidal, apical rounded apically, basal angular basally, 1.2–2 mm long, 1.3–1.6 mm wide, hilum dark brown, prominently raised within a groove, not at all to only slightly extended onto basal or apical surface, testa pale grayish brown, scrobiculate on all surfaces, white-farinose in all depressions, around the embryotega and in the groove around the hilum, the farinose granules rarely confined to the vicinity of the hilum and embryotega (*Verdcourt 1921* and *Faden & Faden 77/611*).

HABITAT.—Lowland and submontane forests, sometimes associated with limestone outcrops, frequently on boulders along streams and at the bases of waterfalls in the Eastern Usambara Mountains, described as "the first invader in a cleared area in evergreen rain forest," on *Greenway 1668;* partial or dense shade; 30–900 m.

FLOWERING.—Flowering specimens have been collected in March, April, June, August–October, and December. Based on two populations in cultivation, the flowers appear to open before to just slightly after dawn. They were observed to fade in the field about 1200 hrs.

CHROMOSOME NUMBER.—$n = 16$, $2n = 32$.

DISTRIBUTION.—Coastal SE Kenya, coastal and subcoastal NE Tanzania (Map 5).

SPECIMENS SEEN.— KENYA. KILIFI: Rabai Hills, Mombaz. (Mombasa), Fimbine? (probably = Fumbini on Kilifi Creek), Jul–Nov 1885, *W.E. Taylor s.n.* (BM); Kaloleni district (i.e., area; erroneously recorded as Kwale District), *Verdcourt 2410* (EA, FT, K). KWALE: Muhaka Forest, 4°20′S, 39°31′E, *Faden & Faden 77/611* (EA, F, K, MO, US); Marenji (Marenje) Forest Reserve, *Verdcourt 1921* (BR, EA, K, PRE).

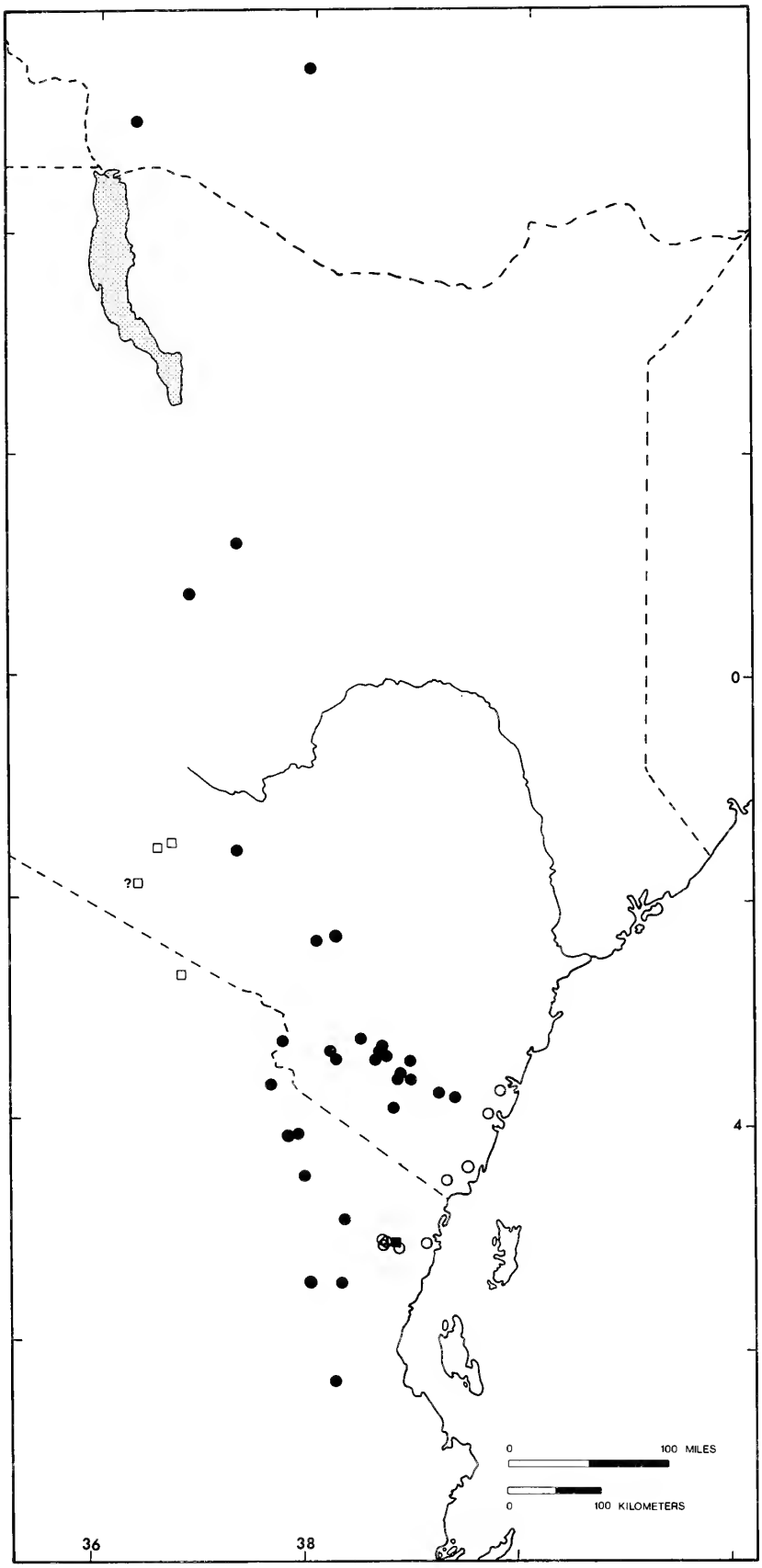
TANZANIA. Without data: *Warnecke 323* (EA). LUSHOTO: Amani, Kwam Kujv (Kwamkuyu), *Engler 3416* (EA); Eastern Usambara Mts., Muheza–Amani road, crossing of Kwamkuyu River, 5°06′S, 38°39′E, *Faden & Faden 74/371* (C, EA, K, MO, US, WAG); Eastern Usambara Mts., Amani, *Greenway 1668* (EA, K, PRE); Eastern Usambara Mts., Sigi, near Amani, cultivated in Nairobi, *Magogo in EA14203* (BR, EA, K, MO); Eastern Usambara Mts., Kwamkuyu Falls, Derema, *Verdcourt 161* (EA, K, MO, PRE); Amani, *Winkler 3638* (WRSL—2 sheets); same locality, *Zimmermann 8231* (EA). TANGA: Magila near Muheza, *Archbold 1408* (EA); Kiomoni Quarries near Tanga, cultivated in Nairobi, *Organ in EA15079* (EA).

DISCUSSION

I could not read the locality starting with "F" on the type specimen. Clarke (1901) interpreted the Rev. Taylor's handwriting as "Fimbine." S.A. Robertson (personal communication) has stated that it is probably Fumbini on Kilifi Creek.

This species has sometimes been confused with others. Brenan (1952) cited two specimens of *A. taylorii, Greenway 1668,* and *Verdcourt 161* (cited as 151), under *Aneilema rendlei,* noting that they had smaller capsules with fewer seeds than other specimens of *A. rendlei.* Morton (1966) identified another collection of *A. taylorii, Verdcourt 2410,* which had been determined in the Kew Herbarium as *A. umbrosum* var. *ovato-oblongum,* as an undescribed species closely related to *A. umbrosum.* Although pressed specimens of *A. taylorii* bear a striking resemblance to some West African plants of *A. umbrosum,* this similarity is superficial. The two species differ in at least 20 floral characters, including lateral stamen filament pubescence and medial stamen anther size, shape, and color. Herbarium specimens of *A. umbrosum* are readily separated by the inflorescence axis and pedicel apex puberulous and the seeds reticulate-foveate.

Aneilema taylorii exhibits a great deal of morphological variation, particularly in size of floral parts. I previously suggested that different-size flowers might be taxonomically significant in this species, with smaller flowers occurring in gracile, narrow-leaved, coastal plants, and larger flowers in more robust, broader-leaved plants from the Eastern Usambara



MAP 5.—Distribution of *Aneilema brenanianum* Faden, new species (open squares), *A. rendlei* C.B. Clarke (solid circles), *A. taylorii* C.B. Clarke (open circles), and *A. usambarense* Faden, new species (solid square).

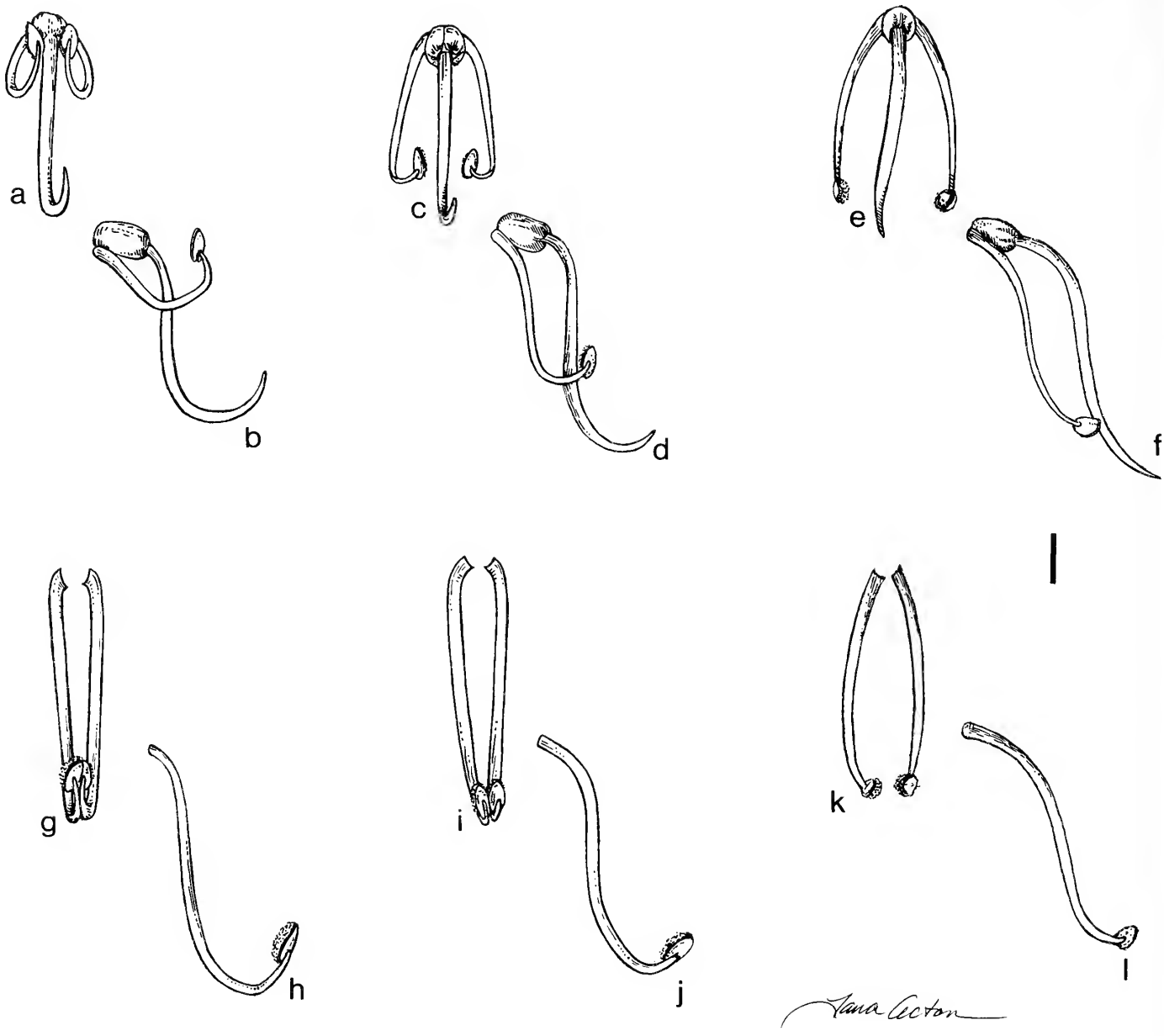


FIGURE 45.—Comparison of *Aneilema rendlei, A. taylorii,* and *A. rendlei* × *taylorii:* lateral stamens and gynoecium. *A. rendlei* C.B. Clarke (*a,b,g,h*): *a,* perfect flower, front view; *b,* perfect flower, side view; *g,* staminate flower, front view; *h,* staminate flower, side view (from *Kabuye & Evans 163*). *A. rendlei* C.B. Clarke × *taylorii* C.B. Clarke (*c,d,i,j*): *c,* perfect flower, front view; *d,* perfect flower, side view; *i,* staminate flower, front view; *j,* staminate flower, side view (from *Kabuye & Evans 163* (*rendlei*) × *Faden & Faden 74/371* (*taylorii*)). *A. taylorii* C.B. Clarke (*e,f,k,l*): *e,* perfect flower, front view; *f,* perfect flower, side view; *k,* staminate flower, front view; *l,* staminate flower, side view (from *Faden & Faden 74/371*). (Bar = 2 mm for all illustrations.)

Mountains (Faden, 1975). A new collection from the Kenya coast, *Faden & Faden 77/611,* has tended to support this hypothesis. First, by being annual—all of the plants found were completely dead, and plants subsequently grown from seeds collected from the dead plants behaved as annuals—this collection agreed with the presumption that all of the Kenya collections, as well as *Organ in EA15079* from Tanzania, were annuals, in contrast to plants from the Usambaras. Second, flower size and floral parts' dimensions in the cultivated plants of *Faden & Faden 77/611* much better agreed with *Organ in EA15079* than with living plants of two Usambara collections, *Magogo in EA14203* and *Faden & Faden 74/371.* While the

new data gained from *Faden & Faden 77/611* would support the recognition of two subspecies in *A. taylorii*, hard and fast characters usable in herbarium specimens have remained elusive. Until such time as some are found or the weight of the floral evidence becomes overwhelming, there is no compelling reason to recognize subspecies that can only be identified by the provenance of the collection, when flowers are not available.

The variation in color of the pollen grains of the middle anther is a phenological phenomenon. When the flowers open all of these pollen grains are yellow. During the course of flowering they change to white, and so, when the flowers begin to fade, only white pollen grains can be found in the middle anther. No such color change occurs in the pollen of the lateral anthers.

The gaps in the monthly flowering records mostly reflect the small number of collections of this species. On the other hand, the lack of flowering specimens from January and February, the driest months through out the range of *A. taylorii*, may well indicate that the species is not in flower during that period.

All of the Tanzanian collections of *A. taylorii* from Lushoto District are from a small area of the Eastern Usambara Mountains centered around Amani, the former German colonial agricultural research station. The species is apparently fairly common in this region between 500–900 m altitude. It is decidedly uncommon throughout the rest of its range.

Aneilema taylorii is undoubtedly most closely related to *A. usambarense*, which may ultimately prove to be conspecific. For distinctions see that species. It is also closely related to *A. rendlei*, and crossing experiments have shown the two species to be interfertile, at least through the F1. Some of the differences between these species are given in the key and under *A. rendlei* (see Figures 44, 45). To these distinctions the following characters of *A. taylorii* can be added: leaf sheaths shorter; inflorescence axis, cincinnus peduncles and axes, pedicels and medial sepal consistently green; lateral staminode filaments less strongly curved, with bases more slender; lateral anthers always facing the floral midplane. Moreover, *A. taylorii* and *A. rendlei* are completely isolated ecologically as well as geographically (Map 5).

2. *Aneilema usambarense* Faden, new species

Aneilema rendlei C.B. Clarke.—Brenan, Kew Bull., 7:196, 1952, p.p.

Herbae perennes decumbentes caulibus ad 90 cm altas, foliis lanceoato-ellipticis, 6.5–16 cm longis, 2–4.5 cm latis, petiolis ad 3.5 cm longos. Inflorescentiae thyrsi ovoidei, glabri, 4–7 cm longi, 4.5–6 cm lati, cincinnis 14–20 compositi. Cincinni pedunculis 5–10 mm longis, bracteolis (2–)3–4(–5) mm distantibus. Pedicelli 6–8 mm longi, glabri; sepala glabra; stamina filamentis glabris. Capsulae 5–6 mm longae, 2.5 mm latae, chocolatinae, glabrae, loculis ventralibus uterque seminibus 4 praeditis. Semina 1.1–1.7 mm longa, 1.5–1.6 mm lata, testis scrobiculatis (Figure 46).

TYPE.—Tanzania, Eastern Usambara Mts., W slope of Mt. Mlinga, 4 Dec 1940, *Greenway 6058* (K, holotype; EA, PRE, isotypes).

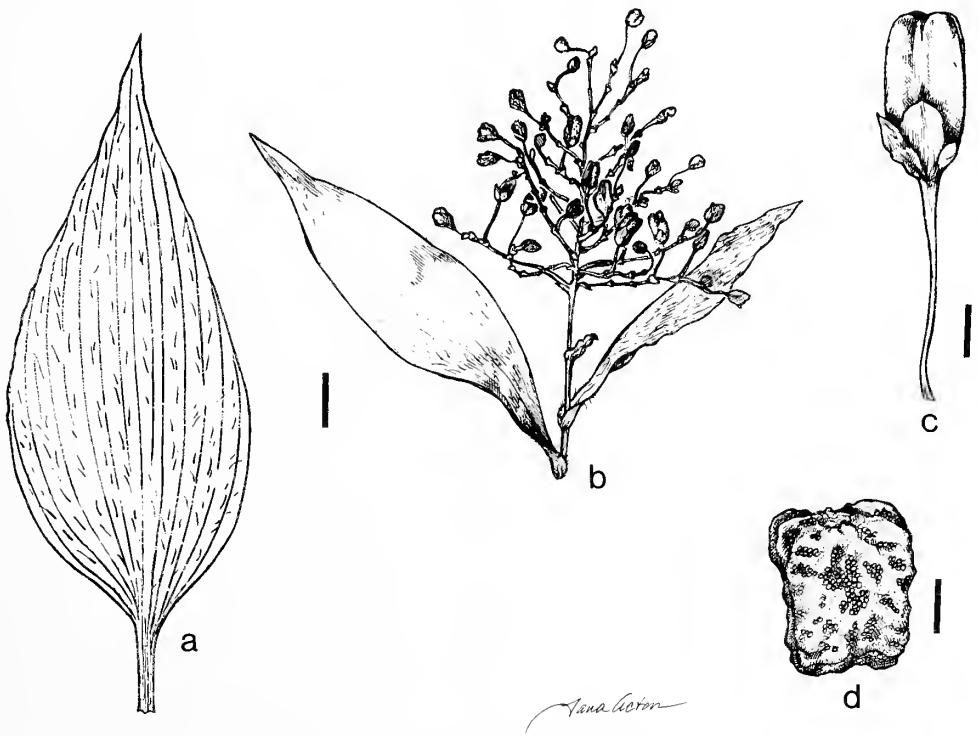


FIGURE 46.—*Aneilema usambarense* Faden, new species: *a*, leaf; *b*, inflorescence; *c*, capsule; *d*, seed (all from *Greenway 6058*). (Bar = 10 mm for *a,b;* 2 mm for *c;* 0.5 mm for *d.*)

Perennial herbs (habit type IA, Figure 1). Roots not seen, probably thin, fibrous. Shoots decumbent, the flowering shoots ascending, to 90 cm tall. Internodes 3.5–10 cm long, pubcrulous to glabrescent. Leavcs spirally arranged, sheaths 0.7–2 cm long, puberulous, ciliate at the apex, laminae petiolate, lanceolate-elliptic, 6.5–16 cm long, 2–4.5 cm wide, apcx acuminate, base cuneate, margin planar, scabrid, adaxial surface patently hirsute-puberulous, the scattcred uniseriate hairs 1.5–2.5 mm long, abaxial surface pilose-puberulous, the hairs more numerous and shorter than those of the adaxial surface and ± confined to the lateral vcins, petioles to 3.5 cm long, ciliate on thc margins.

Inflorescences thyrses (Figure 46*b*), terminal (rarely also axillary from the inflorescence bract), modcrately dense, ovoid, 4–7 cm long, 4.5–6 cm wide, with 14–20 ascending cincinni. Pcduncles 1.5–2.8 cm long, pubcrulous. Inflorcscence bract mcdial, hcrbaccous, vcry rcduced. Inflorescence axis glabrous. Cincinni to 4 cm long and 9-flowered. Cincinnus bracts herbaceous, lowermost sometimes perfoliate, appressed to the cincinnus peduncles, lanceolate-elliptic to ovate, 1–3.5 mm long, glandular near the apex, glabrous. Cincinnus peduncles relatively uniform in length within the inflorescence, exceeding the cincinnus bracts, 5–10 mm long, glabrous. Cincinnus axes glabrous. Bracteoles attached (2–)3–4(–5) mm apart, herbaceous, eccentrically cup-shaped, perfoliate, 1.2–1.5 mm long, 0.4–0.7 mm high, with a prominent subapical gland, glabrous, margin somewhat thickened (glandular?) near the fused edge.

Flowers perfect and staminate. Pedicels 6–8 mm long, aligned with the cincinnus axis in flower, erect in fruit, glabrous. Sepals glandular near the apex, glabrous; medial scpal ~3 mm long, lateral sepals oblong-clliptic, ~3 mm long and 1.5 mm wide. Paired petals ~7 mm long, mauve. Medial petal ovate, 4–5 mm long. All filamcnt bases frec. Medial staminode filamcnt ~1.5 mm long, antherode bilobed, lobes rcniform, ~1–1.5 mm wide, connective elongate. Lateral staminodes with filamcnts question-mark-shapcd, ~5 mm long, anthcrodes bilobcd, lobcs stipitate, ~0.7 mm wide. Lateral stamens with filaments declinate, ~7–8 mm long, glabrous, anther lanceolate-elliptic, 1.5 mm long, 0.7 mm wide. Medial stamen with filament straight, then gently recurved, ~5 mm long, anther 1.8 mm long, with a broad connective. Ovary sessile, ~2 mm long, apparently glabrous, style J-shaped, 8.5 mm long, stigma small.

Capsules sessile (Figure 46*c*), oblong-elliptic, dchiscent, bivalved, bilocular, 5–6 mm long, 2.5–3 mm wide, chocolate brokcn, lustrous, glabrous, apex emarginate, valves pcrsistcnt, dorsal locule obsolcte, ventral loculcs 4-scedcd, cells of the capsule wall transversely elongate. Scods trapczoidal (Figurc 46*d*), apical rounded apically, basal angular basally, 1.1–1.7 mm long, 1.5–1.6 mm wide, hilum black, prominently raised within a groove, not extended onto apical and basal surfaccs, tcsta pale grayish brown, scrobiculate on all surfaces, white-farinose in all dcpressions, around the embryotcga and in the groove around the hilum.

HABITAT.—Shady path sidcs in evergreen forest with *Parinari excelsa, Funtumia latifolia, Sterculia appendiculata, Allanblackia stuhlmannii, Isoberlinia, Schefflera,* growing with *Sacciolepis curvata;* 620 m.

FLOWERING.—The single collection is from December and is flowering and fruiting. The sizes of the inflorescences indicate that the plant was in flower in November and perhaps earlier.

CHROMOSOME NUMBER.—Unknown.

DISTRIBUTION.—Known only from the isolated massif Mt. Mlinga in the Eastern Usambara Mts. in NE Tanzania (Map 5).

SPECIMENS SEEN.—TANZANIA. TANGA: Eastern Usambara Mts., W slope of Mt. Mlinga, *Greenway 6058* (EA, K, PRE).

DISCUSSION

The single collection of *A. usambarense* was treated without comment as *A. rendlei* by Brenan (1952). This is hardly surprising in view of his inclusion of two collections of *A. taylorii* under *A. rendlei.* Brenan's confusion of these three taxa is understandable considering the small number of collections available to him and the somewhat intermediate appearance of *Greenway 6058* between *A. taylorii* and *A. rendlei.*

Two relatively well-preserved flowers on the PRE sheet of *Greenway 6058,* one perfect, the other staminate, suggest that dimorphism in lateral stamen filaments is present and is no greater than that in *A. taylorii.*

Aneilema usambarense is most closely related to *A. taylorii,* but differs in a number of characters. Most importantly, *A. usambarense* has taller flowering shoots, longer leaves with longer petioles, more numerous cincinni in the inflorescence, and darker brown capsules with more numerous seeds per locule. It also has somewhat longer cincinnus peduncles and more widely spaced bracteoles than *A. taylorii.* Possibly other distinguishing characters are present in the flowers, but they could not be dctermined from the dried specimens.

The generally larger size in all of these characters in *A. usambarense* than in *A. taylorii* suggests that *Greenway 6058* might be merely a specimen of the latter from a very favorable habitat or perhaps an ecotype of that species. Because plants of *A. taylorii* (*Faden & Faden 74/371*) have been cultivated under favorable conditions and have failed to significantly reduce the morphological differences between the two species, ecological factors effecting greatcr size seem insufficient to account for the observed diffcrences between *Greenway 6058* and *A. taylorii.* Genetically basod, ecotypic variation cannot be ruled out, but the plant association dcscribed on *Greenway 6058* (see habitat above) is the dominant one in the Amani area of the Eastern Usambara Mountains whcre *A. taylorii* is frequent. There is little reason to expect climatic diffcrences in thcse two areas, only about 5 km apart, to be great enough to account for the observed morphological differences.

Greenway 6058 might also be considercd a possible

autopolyploid of *A. taylorii* or a hybrid between it and *A. rendlei*. Studies of the morphological differences in other supposed autopolyploids in *Aneilema* have not been sufficiently detailed to provide a basis for comparison. In the absence of living material or any clearly supportive data of a polyploid origin, there is no compelling reason for treating the Greenway specimen as having had one.

Aneilema usambarense, from a casual inspection, appears intermediate between *A. taylorii* and *A. rendlei*. It is somewhat intermediate only in the number of cincinni per inflorescence, capsule size and number of seeds per locule. In most other characters, including habit, leaf shape, cincinnus peduncle and pedicel length, seed width, distance between bracteoles and degree of lateral stamen dimorphism, *A. usambarense* is much more similar to *A. taylorii* than to *A. rendlei*. Its distribution and habitat also suggest a closer relationship with *A. taylorii;* a hybrid origin is unlikely.

Artificial hybrids (Figures 44, 45) made between cultivated plants of *A. taylorii* (*Faden & Faden 74/371*) and *A. rendlei* (*Kabuye & Evans 163*) differed from *Greenway 6058* in having broader, stramineous capsules (3.2–3.9 mm wide) and broader seeds (1.65–1.75 mm wide), which further supports the conclusion that *A. usambarense* is not a hybrid between those two species.

Greenway 6058 is best treated as a closely related and probably recent derivative of *A. taylorii*. It could be considered either a subspecies of *A. taylorii* or a closely related species. The latter course has been followed largely for convenience. It was felt that inclusion of *Greenway 6058* in *A. taylorii* would have resulted in a blurring of the distinctions between that species and *A. rendlei*. The peculiarly colored capsules of *Greenway 6058* separate it from both of these species and support its separation at the specific level.

Final determination of the proper status for *A. usambarense* must await the availability of further collections, particularly living material, so that the floral structure and variability can be studied. An attempt by the author to collect this plant in March 1974 was unsuccessful. Unfortunately, the habitat was being destroyed rapidly.

3. *Aneilema rendlei* C.B. Clarke

Aneilema rendlei C.B. Clarke in Thiselton-Dyer, Fl. Trop. Africa, 8:68, 1901 [*Donaldson Smith 346* excl.].—Chiovenda, Webbia, 8:38, 1951, p.p. maj.—Brenan, Kew Bull., 7:196, 1952, p.p.—Cufodontis, Bull. Jard. Bot. Natl. Belgique, 41, suppl., 1518, 1971 [*Donaldson Smith 346* excl.].—Faden in Agnew, Upland Kenya Wild Fl., 666, 1974 [type: Ethiopia (Somaliland on label), 23 Apr 1895, *Donaldson Smith s.n.* (BM)].

Aneilema octospermum C.B. Clarke, in sched. ["octosperma"].—Brenan, Kew Bull., 7:196, 1952 [nom. nud. pro syn.].

Perennial herbs (habit types IB, IC, Figure 1). Roots fibrous, generally produced only at the lower nodes. Shoots erect to ascending or occasionally decumbent, generally 25–100 cm high, much branched at the base, unbranched or sparsely branched above, shoot bases swollen. Internodes (2.5–)4–6(–9) cm long, glabrescent to puberulous. Leaves spirally arranged, sheaths 1–2.5(–3) cm long, puberulous, pilose or pilose-puberulous, ciliate at the apex, laminae petiolate, narrowly lanceolate to lanceolate-elliptic, elliptic or occasionally ovate-elliptic, 2.5–11 cm long, 1–3.5 cm wide, apex acuminate or occasionally acute, base cuneate, margin undulate or planar, scabrid and sometimes ciliate, both surfaces dull, the adaxial patently hirsute-puberulous, with uniseriate hairs to 1.5–3 mm long, abaxial patently pilose-puberulous, with uniseriate hairs shorter and more numerous than those of the adaxial surface, petioles to 1.5(–1.8) mm long, with ciliate margins.

Inflorescences thyrses (Figure 44*a;* Plate 2*d*), terminal and occasionally axillary from the uppermost leaves, moderately dense, ovoid, (2–)3–5(–5.5) cm long, (1.5–)2–3(–6) cm wide, with (9–)13–20(–32) cincinni, alternate to subopposite, ascending. Peduncles (1.5–)4–6(–10.5) cm long, puberulous basally, glabrous apically. Inflorescence bract medial, supramedial or occasionally subapical, herbaceous or less commonly membranous, bract-like or occasionally foliaceous. Inflorescence axis glabrous. Cincinni to 3.5 cm long and 13-flowered. Cincinnus bracts herbaceous, lowermost sometimes perfoliate, appressed to the cincinnus peduncles or rarely reflexed with age, lanceolate or lanceolate-elliptic to oblong or ovate, 1.5–3(–5) mm long, cucullate and glandular subapically, glabrous. Cincinnus peduncles relatively uniform in length within the inflorescence, exceeding the cincinnus bracts, (3–)4–6(–8.5) mm long, glabrous. Cincinnus axes glabrous. Bracteoles attached (1–)2–2.5(–3) mm apart, herbaceous, eccentrically cup-shaped, perfoliate (rarely not perfoliate), 1.2–2.2 mm long, 0.4–1.2 mm high, with a prominent, subapical gland, glabrous, margin sometimes apparently glandularly thickened near the fused edge.

Flowers perfect and staminate, slightly fragrant, 9.5–17 mm wide (Figure 17; Plate 1*o,p*). Pedicels 2.5–4(–5.5) mm long, to 6.5 mm long in fruit, generally held above the cincinnus axis in flower, erect in fruit, persistent, glabrous. Sepals with a prominent subapical, green, inconspicuously bilobed gland, glabrous; medial sepal lanceolate-ovate to ovate-elliptic, 3–4.5 mm long, 2–2.6 mm wide; lateral sepals elliptic to oblong-elliptic, 3–4.5 mm long, 1.7–2.2 mm wide. Paired petals 7.5–11 mm long, 4.5–8 mm wide, limb ovate to ovate-elliptic or suborbicular, 5.5–8 mm long, lilac (RHS colors: 76B, *Kabuye & Evans 163,* cultivated, and *Faden et al. 69/322,* cultivated; 76A-B, *Faden & Faden 74/232* and *Faden et al. 70/157,* cultivated; 76C, *Faden & Faden 72/240,* cultivated; 75A, 76C, 84C, *Faden & Faden 74/281;* 76A, 82C-D, *Faden & Faden 74/503*), veins contrastingly darker than background color, apex rounded, claw 2.5–3 mm long, colorous with limb at apex, shading to greenish yellow at base, glabrous. Medial petal not strongly reflexed, ovate to ovate-elliptic or lanceolate-ovate, 4.5–5.5 mm long, 3–3.5 mm wide, greenish white, sometimes flushed with lilac. All filament bases free. Medial

staminode filament 1.2–2 mm long, yellow, antherode bilobed (Figure 43*c*), lobes stipitate, flat, reniform, 1–1.3 mm long, 1.8–2.5 mm wide, yellow abaxially, yellow with small maroon spots (rarely lacking) adaxially, connective elongate. Lateral staminodes (Plate 1*p*) 4.5–5.5 mm long, question-mark-shaped, very thick at the base, tapering apically, entirely yellow or, greenish yellow at base, flesh pink or pinkish buff in middle, yellow at apex, antherodes bilobed (Figure 43*c*), lobes stipitate, reniform, 0.5–0.8 mm long, entirely yellow or sometimes spotted with maroon on adaxial surface, connective not elongate. Lateral stamens strongly dimorphic in perfect and staminate flowers (Figures 16*b*, 17, 45), filaments glabrous, in perfect flowers parallel or slightly divergent, 5.5–8 mm long, broadly U-shaped, in staminate flowers closely parallel, 9–13 mm long, J-shaped, anthers narrowly elliptic to lanceolate-elliptic, in staminate and some perfect flowers with anther sacs facing the filament bases, in some perfect flowers facing the floral midplane, 1.5–1.7 mm long, 0.6–0.8 mm wide, connective creamy white to gray-green, pollen orange-yellow. Medial stamen with filament 3.5–5 mm long, anther elliptic, 1.7–2 mm long, 1–1.4 mm wide, usually held perpendicular to the ground, sometimes pendulous, connective very convex, creamy white, greenish white or greenish yellow, always with numerous maroon spots, pollen yellow. Ovary sessile, oblong-elliptic, 2–2.5 mm long, 0.9–1.1 mm wide, glabrous except for some very inconspicuous, appressed, glandular microhairs along the lateral sutures and sometimes on the ventral surface (Figure 42*a*), apex rounded, dorsal locule usually represented by a low, middorsal hump or ridge, usually empty, occasionally 1(–3)-ovulate, ventral locules each 3–6-ovulate; style 7.5–10 mm long, J-shaped, sharply deflexed at base, thickest below middle, tapering towards base and apex (Figure 17*a;* Plate 1*p*), held in floral midplane, stigma small, bluish purple, held below the stamens but at some distance from them.

Capsules sessile (Figure 44*c*), oblong to oblong-elliptic, dehiscent, bivalved, 2(–3)-locular, (5–)6–10 mm long, (3.1–)3.5–4.2 mm wide, stramineous, lustrous, glabrous, apex rounded to truncate or emarginate, valves persistent, dorsal locule obsolete or, if present, usually empty, rarely 1-seeded, ventral locules each 3–5-seeded, rarely less by abortion, cells of the capsule wall transversely elongate. Seeds (Figure 44*d;* Plate 5*f*) trapezoidal, apical ventral rounded apically, basal ventral angular basally, 1.5–2.2 mm long, 1.5–2 mm wide, hilum blackish brown, prominently raised within a groove, not at all to only slightly extended onto apical or basal surfaces, testa grayish brown to flesh-pink, scrobiculate on ventral and dorsal surfaces, white-farinose in all depressions, around the embryotega and in the groove around the hilum.

HABITAT.—Dry deciduous bushland and bushland thicket, often on rocky slopes, occasionally along seasonal streams; usually in sandy soil; generally in partial shade; 300–1200 m.

FLOWERING.—Flowering specimens have been seen from all months except August and September. In Kenya and Tanzania there are two chief flowering periods, December–February (following the short rains) and April–June (during and after the long rains). In the field, flowers were observed to open at about 0800 hrs. They probably close 1330–1430 hrs.

CHROMOSOME NUMBER.—$n = 16$, $2n = 32$.

DISTRIBUTION.—SW Ethiopia N and SE Kenya, NE Tanzania (Map 5).

SPECIMENS SEEN.—ETHIOPIA. GEMU-GOFA: Rive del Ghizo, *Corradi 2159,* p.p. (FT) and *2160* (FT). SIDAMO: 23 Apr 1895, *Donaldson Smith s.n.* (BM).

KENYA. KWALE: 2.8 km Samburu-Mackinnon Road, 3°47′S, 39°15′E, *Faden & Evans 70/788* (EA, K); same locality, *Faden & Faden 72/240* (EA, MO); Taru, *Scott Elliot 6179* (K). LAIKIPIA: Colcheccio Ranch, NE corner, between 0°40′N, 36°54′E and 0°44′N, 36°57′E, *A. Faden 27/85* (US). LAIKIPIA/NORTHERN FRONTIER: Near meeting point with Samburu District, Nolaleta River, ~0°44′N, 36°57′E, *A. Faden 16/85* (US). MACHAKOS: Kibwezi, *Dummer 5020* (K); Bushwackers, planted in Nairobi, *Gilbert s.n.* (EA); Machakos, Katumani Experimental Farm, Kaiti, *Thomas 1061b* (EA); Kibwezi, *Tweedie 4036* (K). NORTHERN FRONTIER: Mathews Range, Ngeng, *Newbould 3184* (K). TEITA: Voi, Mazinga (Beehive) Hill, *Bally B8534* (EA, K); Mt. Kasigau, lower slopes, *Bally B12692* (G, K) and *Bally B13592* (EA); Maktau, 26 Oct 1915, *Buchanan s.n.* (BM); Taveta–Voi road, at mile post Taveta 36/Voi 36, ~3°25′S, 38°10′E, *Faden et al. 69/322* (DSM, EA, K, MO, US); 2–3 mi Maungu Station–Rukanga road, *Faden et al. 69/403b* (EA); Maungu Hills, S of Maungu Station on Nairobi–Mombasa road, 3°38′S, 38°44′E, *Faden et al. 70/157* (EA); Tsavo National Park East, Simba Hill, 3°22′S, 38°35′E, *Faden & Faden 74/232* (EA, K, MO); 7.3 km on Voi–Taveta road from Nairobi-Mombasa road, 3°26′S, 38°30′E, *Faden & Faden 74/281* (EA, FT, K, MO, P, PRE, US); 1.5 km from Nairobi–Mombasa road on eastern turnoff to Voi, 3°24′S, 38°35′E, *Faden & Faden 74/503* (C, EA, K, LISC, MO, US); Nairobi–Mombasa road, 11.7 km towards Mombasa past Maungu Station, 3°37′S, 38°50′E, *Faden & Faden 74/1285* (EA, K, MO); Taita Hills, 20 Mar 1906, *Grenfell s.n.* (B, K); Tsavo National Park East, Irima, 3°17′S, 38°22′E, *Hucks 669* (EA, Tsavo Research Centre) (mixture with *A. petersii* subsp. *pallidiflorum*); Maungu, Msafiri *307A* (EA); Voi, *Napier 914* (EA, K); Tsavo National Park East, 10–15 mi from Aruba on road to Buchuma, *Verdcourt 3901* (BR, EA).

TANZANIA. BAGAMOYO: Pongwe, 6°19′S, 38°14′E, *Harris et al. BJH4377* (EA, K). HANDENI: Kwa Mkono [Kwamkono], *Archbold 713* (K); Kideleko, 7 km S of Handeni, *Archbold 1897* (EA). LUSHOTO: Western Usambara Mts., Lushoto–Mombo road, 1.5 mi SW of Gare turnoff, *Drummond & Hemsley 2928* (BR, EA, K). MOSHI: Djalla-Krater [Chala], *Geilinger 4783* (K). PARE: E South Pare Mts., Kisuani-Same, *Greenway 2193* (BM, EA, K, PRE); Kiruru, *Haarer 447* (EA, K, MO) and *1445* (EA, K); 3 km Hedaru–Same road, ~4°30′S, 37°54′E, *Kabuye & Evans 163* (BR, EA, K, MO); Masandari Hill, 6 km SSW of Same, *Wingfield 2899* (EA).

Discussion

The type of *A. rendlei* is recorded by Clarke (1901), Brenan (1952), and Cufodontis (1971) as coming from Somaliland, undoubtedly because of the printed label, "Somaliland, 1895, A. Donaldson Smith," on it. However, there is also a handwritten label with the date "23-4-95." From the account of his journey (Donaldson Smith, 1897), it can be determined that on that date Donaldson Smith was not in Somaliland but in Ethiopia at the foot of the Amaro Mountains (5°29′N, 37°56′10″E, 3670 ft). *Aneilema rendlei* has not been collected in Somalia. On the same day that he collected the type of *A. rendlei*, Donaldson Smith also collected his number 346, which is cited by Clarke (1901) under *A. rendlei* but noted to differ from the type in several characters. *Donaldson Smith 346* (BM) is not related to *A. rendlei;* it is *A. sebitense*, which is described below in section *Lamprodithyros*.

Corradi 2159, cited by Chiovenda (1951) as *A. rendlei*, is a mixed collection, consisting mainly of that species but also including a shoot of *A. recurvatum*.

Brenan (1952) supplied a detailed description of *A. rendlei* but unfortunately based it in part on several specimens that do not belong to this species. *Greenway 1668* and *Verdcourt 161* (cited as 151) are *A. taylorii*. *Greenway 6058* is described above as *A. usambarense*.

Aneilema octospermum was intended by Clarke to be based upon *Grenfell s.n.* (K). This specimen falls well within the range of *A. rendlei*.

Among collections with atypical features, *Verdcourt 3901* and *Newbould 3184* have unusually narrow leaves. *Faden & Evans 70/788* and *Faden & Faden 72/240*, both from the same population, have bracteoles that regularly are not perfoliate, a feature otherwise unknown in this species. In all other characters these four collections are typical of *A. rendlei*.

The two populations in which variation in lateral petal color was noted were both large. In contrast, the color in *Faden & Faden 74/232* was determined from a single plant in a small population. Those in *Kabuye & Evans 163* and the other cultivated collections were based on material that was probably genetically uniform. The yellow flower color recorded on *Bally B8534*, is obviously an error.

Capsules are almost always confined to the lower cincinni in the inflorescence. This indicates that the upper cincinni rarely produce perfect flowers. Although plants cultivated in Nairobi did occasionally produce some perfect flowers on the upper cincinni, further field observations are required to determine whether this occurs under natural conditions.

Small, erect, unbranched plants 1.5–5.5 cm tall have been found associated with larger plants of this species. These small plants have the characteristic swollen shoot bases of *A. rendlei* and are considered to be first-year seedlings. Such seedlings are able to survive long, dry periods because they store water in the stem and have reduced transpiration in the dry season due to the die off of the laminae and to the presence of overlapping, papery, persistent sheaths covering the stem. A number of such plants, apparently in good condition, were found in the Tsavo area of Kenya in March 1974, at the end of a longer than usual dry season. Plants of this species may take several growing seasons to mature.

This species most commonly occurs from 500–700 m altitude in Tanzania and southeastern Kenya. The five collections from above 1000 m have come mainly from northern Kenya and Ethiopia. The altitude recorded on *Greenway 2193* should be 3000 ft, not 300 ft.

Aneilema rendlei has several attributes that are rare in the genus. The contrasting veins in the paired petals has not been observed in any other species. Other unusual characters of *A. rendlei* and their distribution within the genus are swollen perennial shoot bases (also in *A. petersii* subsp. *petersii*); maroon-spotted staminode lobes (*A. taylorii*); J-shaped lateral stamen filaments and style (*A. brenanianum, A. taylorii*, and probably *A. usambarense*); a large ellipsoid medial anther with a very convex, maroon-spotted connective (*A. brenanianum, A. taylorii*, and probably *A. usambarense*); only glandular microhairs on the ovary (*A. brenanianum, A. johnstonii*, and *A. taylorii*). The high degree of stamen dimorphism in *A. rendlei* is approached only in *A. brenanianum*.

Aneilema rendlei is most closely related to *A. brenanianum, A. taylorii*, and *A. usambarense*. *Aneilema brenanianum* differs from *A. rendlei* in its habit rhizomatous, roots tuberous, shoots more erect, sheaths becoming papyraceous and completely covering the older parts of the shoots (occurring in *A. rendlei* only in seedlings), laminae sessile and usually lacking long, uniseriate hairs, paired petals white to very pale bluish purple, pedicels longer, capsules broader and seeds larger. *Aneilema taylorii* diverges from *A. rendlei* in its habit decumbent, shoot bases not swollen, thyrses less dense and with fewer cincinni, lateral stamens less dimorphic, fruiting pedicels often decurved, capsules smaller and with fewer, smaller seeds. For differences between *A. usambarense* and *A. rendlei* see the key.

4. *Aneilema brenanianum* Faden, new species

Aneilema sp. A Faden in Agnew, Upland Kenya Wild Fl., 664, 666, 1974.

Herbae perennes rhizomatosae radicibus tuberosis, parte inferiore perenni caulium aeriorum vaginis foliorum papyraceis imbricatis inclusa. Folia laminis lineari-lanceolatis ad anguste lanceolato-ellipticas, (3-)6–15 cm longis, (0.4-)0.6–2.1 cm latis, sessilibus. Inflorescentiae thyrsi, 2–5(-7.5) cm longi; 1.5–4(-5) cm lati, cincinnis (5-)7–20(-24) compositi. Axis inflorescentiae puberulus. Cincinni pedunculis (2-)4–7(-8) mm longis, bracteolis (1-)1.5–4 mm distantibus. Pedicelli 5–12 mm longi. Petala lateralia alba vel albida, 4–8.5 mm lata. Capsulae 6–11 mm longae, 4–5 mm latae, glabrae, loculis ventralibus uterque 3(-4)-seminalibus. Semina 2.1–2.5(-2.9) mm longa, 1.8–2.4 mm lata, testa scrobiculatis (Figure 47).

Type.—Kenya, Masai District (Kajiado District on label),

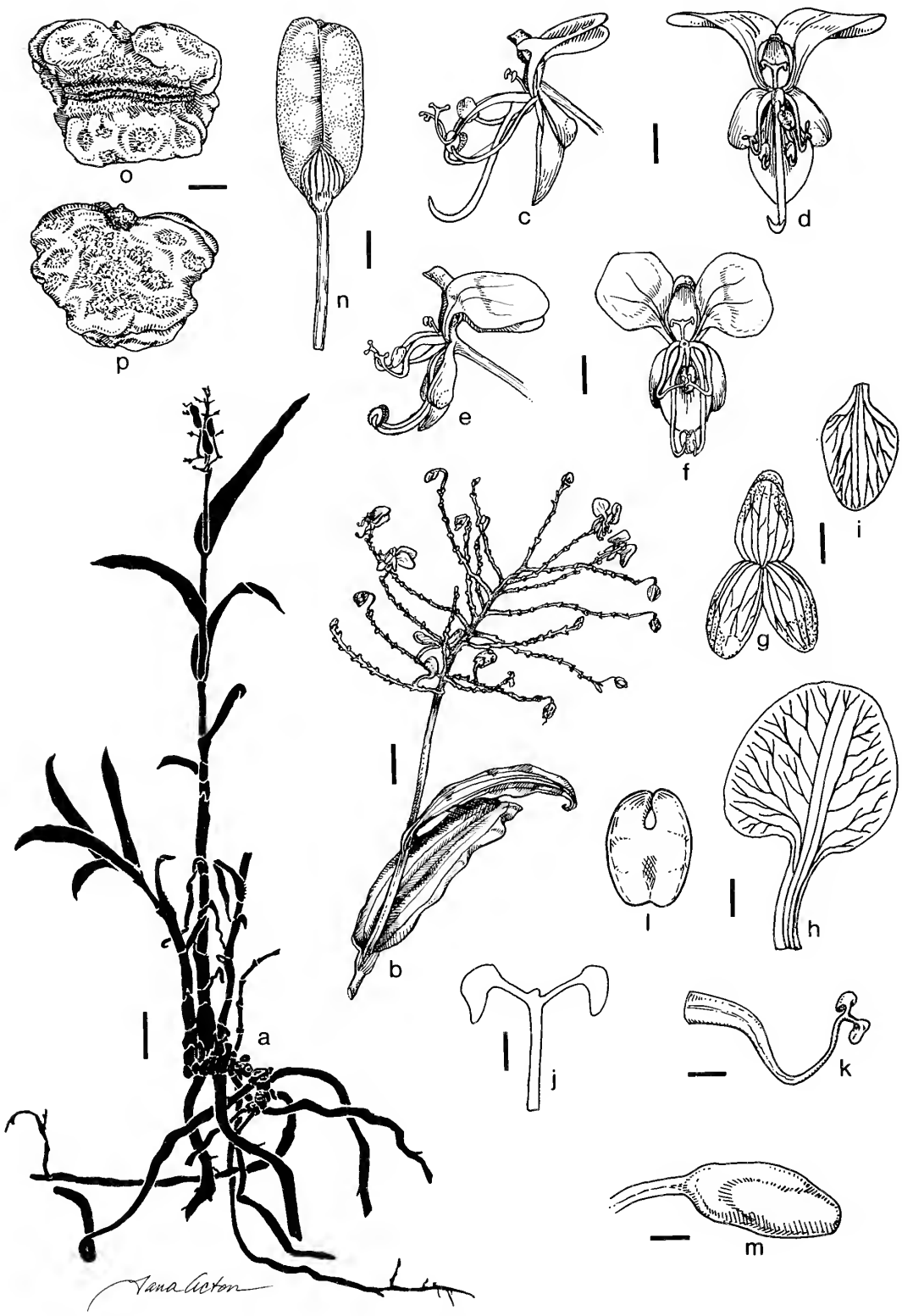


FIGURE 47.—*Aneilema brenanianum* Faden, new species: *a*, habit; *b*, inflorescence; *c*, perfect flower, side view; *d*, perfect flower, front view; *e*, staminate flower, side view; *f*, staminate flower, front view; *g*, calyx, front view; *h*, lateral petal; *i*, medial petal; *j*, medial staminode; *k*, lateral staminode; *l*, medial stamen anther; *m*, ovary and base of style, side view; *n*, capsule; *o*, seed, ventral view; *p*, seed, dorsal view (*a,c-f,j,m-p*, from *Faden & Faden 72/166; b,g-i,k,l*, from *Faden et al. 69/2069*). (Bars = 20 mm for *a;* 10 mm for *b;* 2 mm for *c-f,n;* 1 mm for *g-k;* 0.5 mm for *l,m,o,p*.)

Plates 1–7

PLATE 1.—Flowers of *Aneilema* species. Sections *Aneilema, Amelina,* and *Rendlei* (in part). Section *Aneilema:* (*a,b*) *A. acuminatum* R. Brown: *a,* perfect flower, front view; *b,* perfect flower, top view, showing reflexed medial petal (from *Blaxell 1091*); *c, A. neocaledonicum* Schlecter, perfect flower, front view (from *Bierhorst in Kew Accession No. 000-69.12046*). Section *Amelina: d, A. johnstonii* K. Schumann, perfect flower, top view (from *Faden & Faden 74/490*); (*e,f*) *A. gillettii* Brenan: *e,* perfect flower, front view; *f,* perfect flower, side view (from *Friis 1044*); (*g,h,l*) *A. hockii* De Wildeman: *g,* inflorescence, showing perfect and staminate flowers; *h,* perfect flower, top view; *l,* pistillate flower, side view (*g* from *Faden & Faden 74/1182, h* from *Faden & Faden 74/1065, l* from *Faden et al. 72/234*); *i, A. aequinoctiale* (P. de Beauvois) G. Don, perfect flower, top view (from *Faden et al. 71/922*); *j, A. nyasense* C.B. Clarke var. *brevisepala* Brenan, perfect flower, side view (from *Faden et al. 70/369*); *k, A. longirrhizum* Faden, perfect flower, front view (from *Faden & Faden 74/217*). Section *Rendlei:* (*m,n*) *A. taylorii* C.B. Clarke: *m,* perfect flower, front view; *n,* perfect flower, side view (from *Faden & Faden 74/371*); (*o,p*) *A. rendlei* C.B. Clarke: *o,* perfect flower, front view; *p,* perfect flower, side view (from *Kabuye & Evans 163*).

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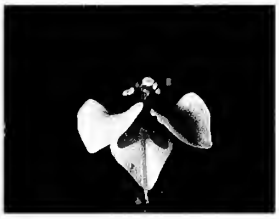

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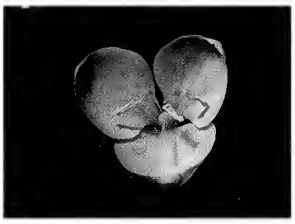

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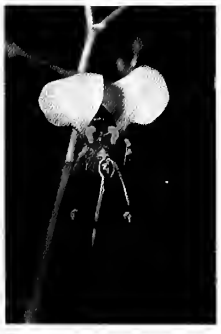

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PLATE 2.—Flowers of *Aneilema* species. Sections *Rendlei* (in part), *Somaliensia*, and *Lamprodithyros* (in part). Section *Rendlei:* (*a–c*) *A. brenanianum* Faden: *a*, habit, showing lower portions of stems covered by long, overlapping sheaths; *b*, perfect and staminate flowers, side views; *c*, inflorescence (from *Faden & Faden 72/166*); *d*, *A. rendlei* C.B. Clarke, inflorescence, showing perfect and staminate flowers (from *Faden et al. 69/322*). Section *Somaliensia:* (*e–g*) *A. somaliense* C.B. Clarke: *e*, inflorescence; *f*, pistillate flower, front view; *g*, perfect flower, front view (from *Faden & Faden 74/923*); (*h,l*) *A. longicapsa* Faden: *h*, perfect flower, front view; *l*, perfect flower, side view (from *Gillett & Beckett 23289*); (*i,j*) *A. pusillum* Chiovenda subsp. *pusillum*): *i*, habit; *j*, perfect flower, front view (from *Gillett et al. 22597*); *k*, *A. pusillum* Chiovenda subsp. *thulinii* Faden, perfect flower, front view (from *Thulin & Warfa 5320*). Section *Lamprodithyros:* (*m,n*) *A. petersii* (Hasskarl) C.B. Clarke subsp. *petersii: m*, inflorescence; *n*, perfect (lower) and staminate (upper) flowers, front view (*m* from *Faden et al. 69/453; n* from *Andrews s.n.*); (*o,p*) *A. petersii* (Hasskarl) C.B. Clarke subsp. *pallidiflorum* Faden: *o*, inflorescence, showing erect inflorescence bract serving as a background for the flowers; *p*, perfect flower, front view (*o* from *Faden & Faden 74/246; p* from *Faden & Faden 74/237*).

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PLATE 3.—Flowers of *Aneilema* species. Section *Lamprodithyros* (in part): *a*, *A. indehiscens* Faden subsp. *indehiscens*, perfect flower, front view (from *Faden & Faden 72/72*); *b*, *A. indehiscens* Faden subsp. *keniense* Faden, perfect flower, front view (from *Faden & Faden 77/788*); (*c*,*d*) *A. recurvatum* Faden: *c*, perfect flower, showing lateral stamens retained in lower petal, side view; *d*, perfect flower, stamens released, side view (from *Faden et al. 69/1066*); *e*, *A. sebitense* Faden, perfect flower, front view (from *Gilbert & Thulin 266*); *f*, *A. forskalii* Kunth, perfect flower, front view (from *Gilbert & Thulin 969*); *g*, *A. woodii* Faden × *forskalii* Kunth, perfect flower, front view (from *Wood 2616A*); *h*, *A. woodii* Faden, perfect flower, front view (from *Wood 2616B*); (*i-l*) *A. tanaense* Faden: *i*, habit; *j*, terminal inflorescence on primary shoot; *k*, perfect flower showing lateral stamens retained in lower petal, front view, *l*, perfect flower, stamens released, front view (*i*,*k*,*l* from *Faden & Faden 74/1053; j* from *Faden & Faden 74/1185*); (*m–o*) *A. calceolus* Brenan: *m*, mat-forming habit; *n*, perfect flower, front view; *o*, perfect flower, side view (*m* from *Faden & Faden 74/1069; n* and *o* from *Organ in EA14970*); *p*, *A. clarkei* Rendle, shoot with two inflorescences, each with one perfect flower (from *Faden & Faden 71/809*).

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PLATE 4.—Flowers of *Aneilema* species. Sections *Lamprodithyros* (in part), *Brevibarbata,* and *Pedunculosa.* Section *Lamprodithyros:* (*a–c*) *A. lamuense* Faden: *a,* habit; *b,* staminate flower, top view; *c,* staminate flower, side view (from *Faden & Faden 74/1083*); *d, A. clarkei* Rendle, perfect flower, front view (from *Faden & Faden 74/1215*); (*e,f*) *A. succulentum* Faden: *e,* shoot with three inflorescences, each with one perfect flower; *f,* perfect flower, front/side view (from *Faden & Evans 70/782*); (*g,h*) *A. zebrinum* Chiovenda: *g,* flowering shoot; *h,* perfect flower, top/side view (from *Faden et al. 70/183*). Section *Brevibarbata: i, A. beniniense* (P. de Beauvois) Kunth, inflorescence (from *Faden et al. 60/1073*); *j, A. welwitschii* C.B. Clarke, perfect flower, front view (from *Faden & Faden 74/157*); *k, A. pomeridianum* Stanfield & Brenan, staminate flower, front view (from *Lock s.n.*); *l, A. brunneospermum* Faden, perfect flower, front view (from *Faden et al. 74/209*). Section *Pedunculosa: m, A. leiocaule* K. Schumann, inflorescence (from *Faden & Evans 70/49; n, A. chrysopogon* Brenan, staminate flower, front view (from *Faden & Faden 74/142; o, A. hirtum* A. Richard, inflorescence showing cincinnus bracts and bracteoles terminating in clavate glands (from *Pawek s.n.*); *p, A. nicholsonii* C.B. Clarke, perfect flower, front view (from *Faden et al. 74/192*).

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PLATE 5.—Seeds of *Aneilema* species: *a*, *A. taylorii* C.B. Clarke (from *Faden & Faden 74/371*); *b*, *A. brenanianum* Faden (from *Faden et al. 69/2069*); *c*, *A. grandibracteolatum* Faden (from *Glover & Gilliland 408*); *d*, *A. ephemerum* Faden (from *Faden & Faden 74/794*); *e*, *A. hockii* De Wildeman (from *Faden & Faden 74/215*); *f*, *A. rendlei* C.B. Clarke (from *Faden et al. 69/322*); *g*, *A. somaliense* C.B. Clarke (from *Faden & Faden 74/923*); *h*, *A. pusillum* Chiovenda subsp. *pusillum* (from *Paoli 1277*); *i*, *A. longirrhizum* Faden (from *Faden & Faden 74/217*); *j*, *A. hockii* De Wildeman (from *Faden & Faden 74/1065*). (a = apical ventral locule seed, b = basal vental locule seed, m = medial ventral locule seed, o = ventral locule seed from one-seeded locule, u = unifferentiated ventral locule seed.) (All to the same scale.)

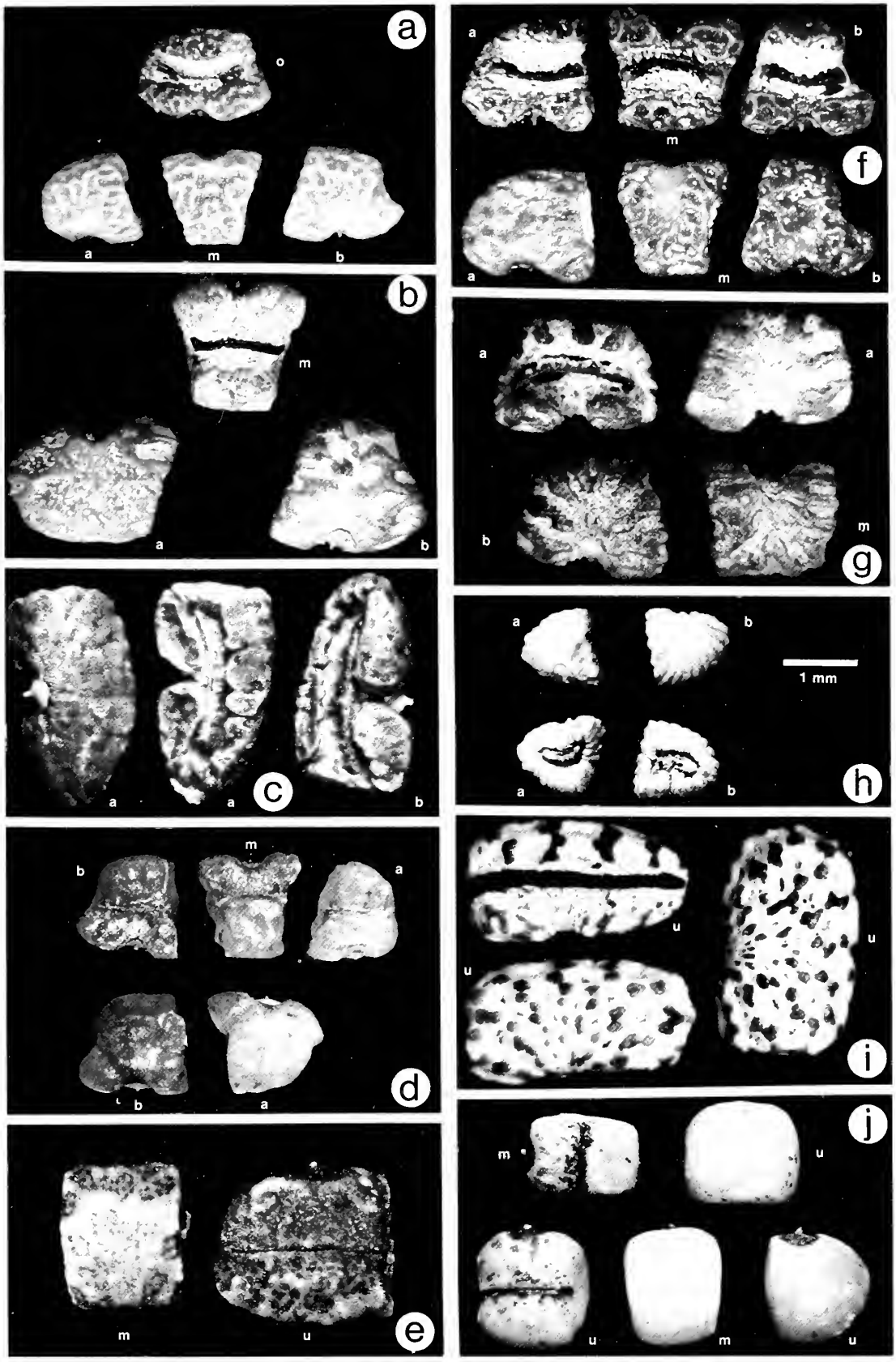
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PLATE 6.—Seeds of *Aneilema* species: *a*, *A. petersii* (Hasskarl) C.B. Clarke subsp. *pallidiflorum* Faden (from *Faden & Faden 74/753*); *b*, *A. indehiscens* Faden subsp. *lilacinum* Faden (from *Faden & Faden 74/202*); *c*, *A. recurvatum* Faden (from *Faden 69/1300*); *d*, *A. forskalii* Kunth (from *Maffey 51*); *e*, *A. benadirense* Chiovenda (from *Ciferri 73*); *f*, *A. calceolus* Brenan (from *Faden & Faden 74/333*); *g*, *A. tanaense* Faden (from *Gillett 19973*); *h*, *A. clarkei* Rendle (from *Faden et al. 71/633*); *i*, *A. lamuense* Faden (from *Faden & Faden 74/1083*); *j*, *A. succulentum* Faden (from *Faden et al. 70/937*). (a = apical ventral locule seed, b = basal ventral locule seed, m = medial ventral locule seed, o = ventral locule seed from one-seeded locule, d = dorsal locule seed.) (All to the same scale.)

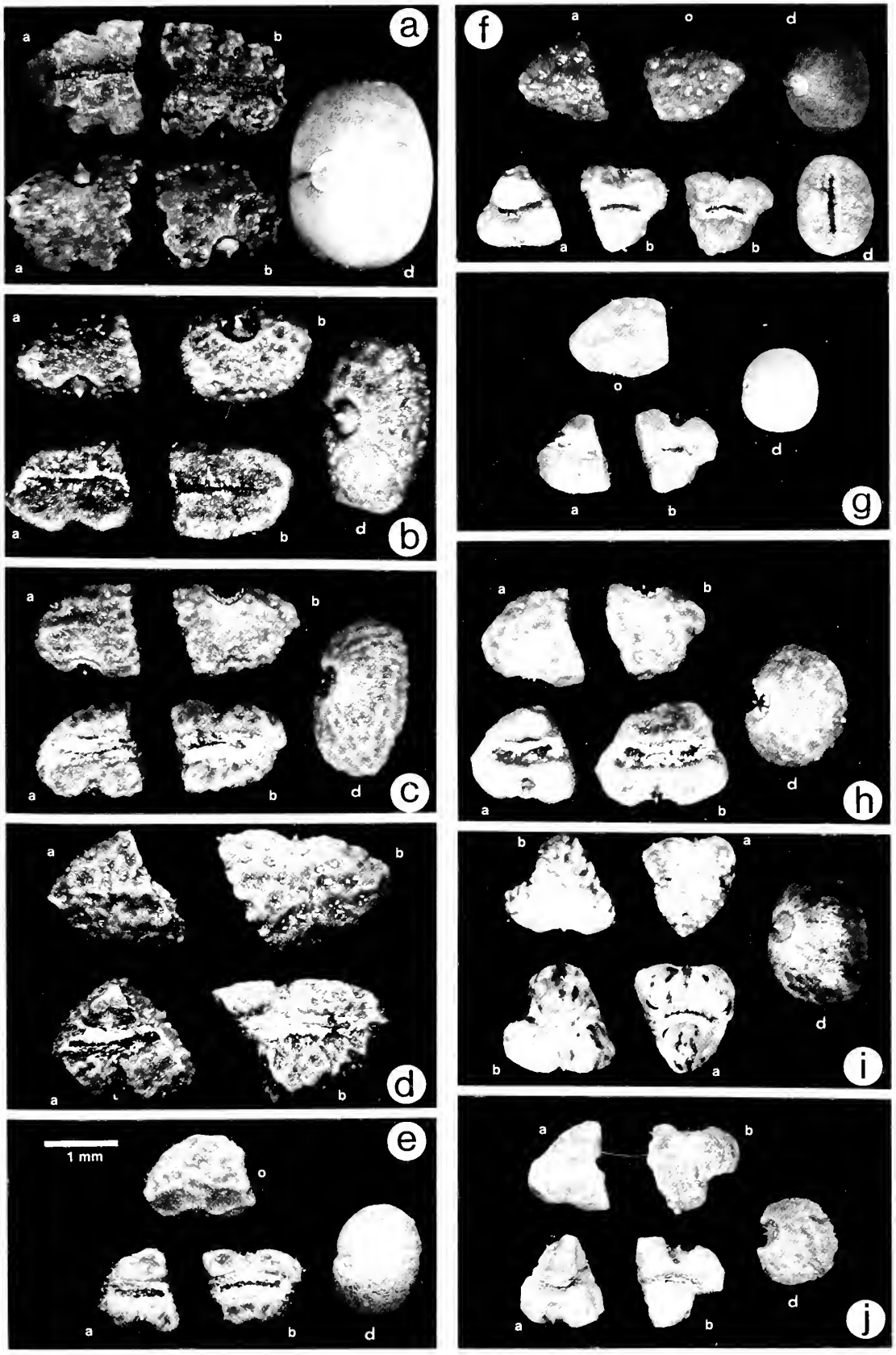
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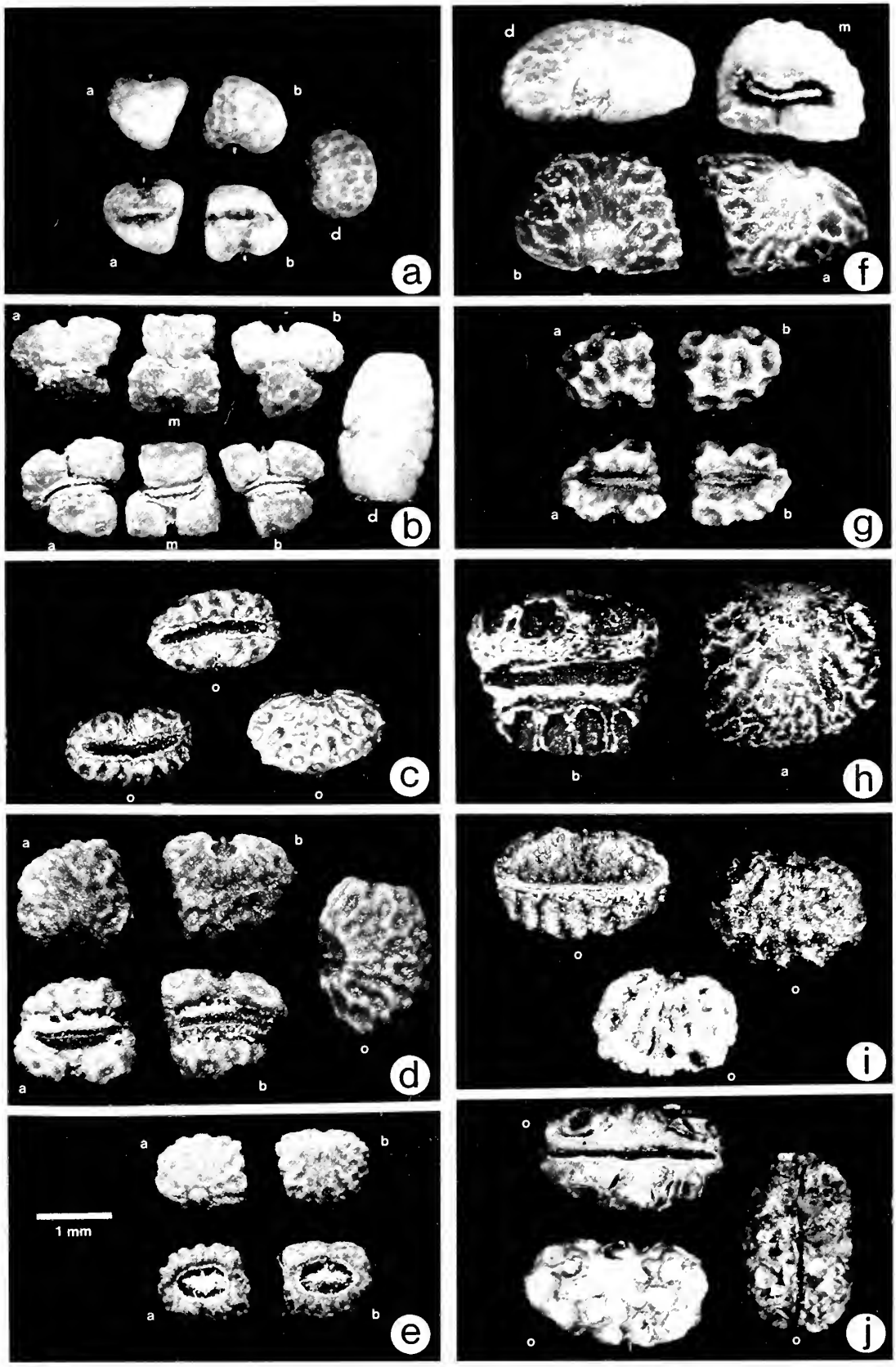
PLATE 7.—Seeds of *Aneilema* species: *a, A. zebrinum* Chiovenda (from *Faden & Faden 74/1052*); *b, A. nicholsonii* C.B. Clarke (from *Faden et al. 74/192*); *c, A. minutiflorum* Faden (from *Paget-Wilkes A*); *d, A. hirtum* A. Richard (from *Milne-Redhead & Taylor 10242*); *e, A. richardsiae* Brenan (from *Richards 9960A*); *f, A. johnstonii* K. Schumann (from *Faden & Faden 74/110*); *g, A. umbrosum* (Vahl) Kunth subsp. *ovato-oblongum* (P. de Beauvois) J.K. Morton (from *Lye & Katende 6235*); *h, A. welwitschii* C.B. Clarke (from *Faden & Faden 74/157*); *i, A. brunneospermum* Faden (from *Faden et al. 74/209*); *j, A. arenicola* Faden (from *Faden & Faden 74/211*). (a = apical ventral locule seed, b = basal ventral locule seed, m = medial ventral locule seed, o = ventral locule seed from one-seeded locule, d = dorsal locule seed.) (All to the same scale.)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mile 35-36 on Nairobi-Magadi road, 14 Dec 1969, *Faden, Evans & Lye 69/2069* (US, holotype; EA, K, MO, isotypes).

Perennial herbs (habit type IVB2, Figures 3, 47*a;* Plate 2*a*). Roots tuberous, brown, to 7 mm thick at base, slightly tapering from there or uniform in thickness for most of their length, to 20 cm long, distal swellings absent. Rhizomes subterranean, unbranched or little branched, moniliform, each segment producing 1-several roots and usually only one aerial shoot. Aerial shoots erect to ascending, rarely straggling, sparsely branched, 15-60(-100) cm tall, the ends dying back to a stiff, perennial, sometimes semi-woody, basal portion. Internodes (1-)1.5-6 cm long, green, those in lower, perennial part of shoots glabrous, completely covered by overlapping, persistent leaf sheaths (Plate 2*a*), those near the inflorescences puberulous, exposed. Leaves spirally arranged, sheaths 1-8.5 cm long, those in lower part of shoot usually greatly overlapping, ribbed longitudinally, becoming gray and papyraceous, persistent, puberulous or glabrescent, sparsely ciliate at the apex in young leaves, laminae sessile, linear-lanceolate to narrowly lanceolate-elliptic, (3-)6-15 cm long, (0.4-)0.6-2.1 cm wide, apex acute to acuminate, base narrowly cuneate, margin usually planar, rarely somewhat undulate, scabrid with a mixture of hook-hairs and prickle-hairs, except near the apex where only prickle-hairs present, both surfaces puberulous, abaxial rarely also with a few longer, uniseriate hairs less than 1 mm long.

Inflorescences thyrses (Figure 47*b;* Plate 2*c*), terminal, moderately dense, ovoid to ovoid-ellipsoid, 2-5(-7.5) cm long, 1.5-4(-5) cm wide, with (5-)7-20(-24) cincinni, alternate or subopposite, ascending. Peduncles 2.5-8(-10.5) cm long, puberulous. Inflorescence bract medial or supramedial, herbaceous or membranous, generally very reduced, sometimes foliaceous. Inflorescence axis puberulous. Cincinni to 3 cm long and 9-flowered. Cincinnus bracts membranous, lowermost sometimes perfoliate, patent or appressed to the cincinnus peduncles or sometimes reflexed, lanceolate to ovate, 2.5-4(-7) mm long, glandular near the apex and frequently along the margin toward the base, glabrous or lower ones sparsely puberulous basally. Cincinnus peduncles relatively uniform in length within the inflorescence, usually exceeding the cincinnus bracts, (2-)4-7(-8) mm long, puberulous. Cincinnus axes puberulous. Bracteoles attached (1-)1.5-4 mm apart, herbaceous, eccentrically cup-shaped, perfoliate, 1.8-2.3 mm long, 0.8-1 mm high, with a prominent gland near the apex and usually smaller glands along the margins especially towards the fused edge.

Flowers perfect and staminate (Figure 47*c-f;* Plate 2*b*), slightly fragrant, 12-14.5 mm wide. Pedicels 5-7.5 mm long in flower, to 12 mm long in fruit, aligned with the cincinnus axis or above it in flower, erect in fruit, persistent, glabrous or with a few minute hairs at the apex. Sepals with a prominent, subapical, green gland; medial sepal ovate, 3-3.7 mm long, 2-3 mm wide, glabrous or rarely with a few minute hairs at the base, gland inconspicuously bilobed; lateral sepals ovate-elliptic to oblong-elliptic, 3-3.7 mm long, 1.9-2.3 mm wide, glabrous, gland unlobed (rarely bilobed). Paired petals 7-10.5 mm long, 4-8.5 mm wide, limb ovate or broadly ovate to suborbicular, 5-7.5 mm long, white or whitish (very pale bluish purple), the latter color often noticeable (or appearing?) only when the flowers fade, apex rounded, claw 2-4 mm long, concolorous with limb, glabrous. Medial petal reflexed, ovate to ovate-elliptic, 3-5 mm long, 2-4 mm wide, greenish white. All filament bases free. Medial staminode (Figure 47*j*) entirely yellow, filament 0.6-1.1 mm long, antherode bilobed, lobes stipitate, flat, ovate or reniform, 0.5-0.9 mm long, 0.5-1.3 mm wide, connective elongate. Lateral staminodes (Figure 47*k*) with filaments 6.5-8 mm long, question-mark-shaped, very thick at base, tapering apically, entirely yellow or tinged with flesh pink subapically, antherodes bilobed, yellow, lobes stipitate, obovate or elliptic, 0.2-0.4 mm long, connective not elongate. Lateral stamens dimorphic in perfect and staminate flowers (Figure 47*c-f;* Plate 2*b*), parallel or slightly divergent, 5-7 mm long (somewhat longer in staminate flowers than perfect flowers), J-shaped, ± pointing forward and downward, then recurved at the apex in the perfect flowers, similarly curved but strongly deflexed near the base and with a larger hook near the apex in the staminate flowers, glabrous, anthers elliptic to lanceolate-elliptic, 1.3-1.9 mm long, 0.7-1 mm wide, pollen creamy white. Medial stamen with filament 3-4 mm long, tapered from a thick base to apex, anther broadly elliptic or ovate, 1.4-1.9 mm long, 1-1.4 mm wide, usually pendulous with the pollen sacs facing upward, connective very convex, pearly white or cream with maroon spots, pollen creamy yellow. Ovary sessile, oblong-elliptic, 2-2.3 mm long, 1-1.3 mm wide, glabrous except for some inconspicuous, appressed glandular microhairs scattered all over or ± confined to the ventral surface and lateral sutures, apex rounded, dorsal locule represented by a low middorsal hump or ridge, empty, ventral locules each 3-4-ovulate; style 6-7 mm long, J-shaped, held in floral midplane, in lateral view thickest in the middle and tapering towards base and apex, stigma small, held below the anthers but at some distance from them.

Capsules sessile (Figure 47*n*), oblong-elliptic, dehiscent, bivalved, bilocular, 6-11 mm long, 4-5 mm wide, stramineous, lustrous, glabrous, apex obtuse to rounded or truncate, valves persistent, dorsal locule obsolete, ventral locules each 3(-4)-seeded, cells of the capsule wall transversely elongate. Seeds (Figure 47*o,p;* Plate 5*b*) trapezoidal, apical ventral rounded apically, basal ventral angular basally, 2.1-2.5(-2.9) mm long, 1.8-2.4 mm wide, hilum black, prominently raised within a groove, slightly extended onto apical and basal surfaces, testa tan, scrobiculate on all surfaces, the depressions often partially uniting on the dorsal surface, forming larger, irregular depressions, white-farinose in all depressions, around the embryotega and in the groove around the hilum.

HABITAT.—Rocky hillsides with numerous boulders and covered by *Acacia-Grewia* or *Acacia-Commiphora,* thorny, deciduous bushland, or occasionally dry plains; sandy soil; partial shade; (600?-)1150-1500 m.

FLOWERING.—Flowering specimens have been seen from December–April and June. Flowers of *Faden & Faden 72/166* opened at 1145 hrs in the field on a hot, sunny day. Those of *Faden & Evans 71/498* did not open until 1700 hrs on a cool, overcast day. The normal opening time is probably about 1200 hrs. Fading time has not been noted.

CHROMOSOME NUMBER.—$2n = 32$.

DISTRIBUTION.—Very local in S central Kenya (eastern edge of Rift Valley) and adjacent Tanzania (Map 5).

SPECIMENS SEEN.—KENYA. MASAI: Nairobi–Magadi road 55.4 km, ~1°30′S, 36°36′, *Faden & Evans 71/513* (BR, C, EA, FT, K, MO, PRE, US, WAG); mi 35–36 on Nairobi–Magadi road, *Faden et al. 69/2069* (EA—2 sheets, K, MO, US); Nairobi-Magadi road 55.4 km, *Faden & Faden 72/166* (BR, EA, K, MO, US); 16 mi from Kiserian towards Magadi on Nairobi–Magadi road, *Faden & Napper 69/238* (EA, K); 17 mi from Kiserian towards Magadi on Nairobi–Magadi road, *Faden & Napper 69/251* (EA, K); Magadi, Jan 1962, *Heriz Smith s.n.* (EA); Nairobi–Magadi road mi 32, *Napper et al. 1877* (EA, K); Nairobi-Olorgasailie [Olorgesailie], mi 38, 1°33.5′S, 36°29′E, *Napper et al. 1999* (EA, K); 37 mi from Nairobi on Magadi road, *Verdcourt et al. 2667* (EA, K, PRE).

TANZANIA. MASAI: Longido, just below water tank of Longido (town), 2°43′S, 36°42′E, *Faden & Evans 71/498* (EA, K, MO, US); bottom slopes of Mt. Longido near new water tanks, *Verdcourt 2531* (EA, K, PRE).

DISCUSSION

This species is named in honor of the late J.P.M. Brenan in recognition of his outstanding contributions to our knowledge of the Commelinaceae, especially of Africa, and for his encouragement of my studies of the family.

The EA and K sheets of *Verdcourt 2531* do not clearly exhibit the papery, overlapping sheaths characteristic of *A. brenanianum*. The flowering shoots in these specimens, however, have grown directly from the rhizome. This is evidenced by the lower leaves still having their laminae. Apparently the plants were collected fairly early in the growing season because only immature capsules are present. The sheaths have not yet turned gray or papyraceous. The PRE sheet of this collection is more typical of the species, the flowering shoots having arisen from an older shoot base covered by gray, papery sheaths.

The habitats in the Kenyan and Tanzanian localities for *A. brenanianum* are quite similar, with *Acacia brevispica*, *A. senegal*, *A. thomasii*, and *Acalypha fruticosa* being common in both. The Kenyan localities also have *Acacia mellifera* and *Grewia* species as dominants, while the Tanzanian locality has *Commiphora* species common in addition to the *Acacia* species. The mean annual rainfall in these areas is 250–500 mm (*Mean Annual Rainfall Map of East Africa*, 1959), with the bulk of the precipitation falling in March to May and October to December (*National Atlas of Kenya*, 1970).

Plants of *A. brenanianum* nearly always grow with their roots in crevices between boulders, making them almost impossible to extract whole. This adaptation allows them to accumulate additional moisture in the form of runoff and probably tends to reduce water loss in the dry season. It may also serve as a protection against root-eating rodents such as mole rats (Bathyergidae). The succulent roots and rhizomes function as storage organs between rainy seasons.

The growth habit of *A. brenanianum* is an adaptation to short and unpredictable growing periods followed by long dry seasons. The overlapping, papery leaf sheaths that cover the lower internodes of the aerial shoots probably reduce transpiration and enable these shoot bases to survive long, dry periods. This covered-internode growth precedes the exposed-internode growth that leads to flowering, although a certain amount of the latter is produced concurrently from the previous growing season's persistent shoots. The exposed internode portions of the shoots, whether flowering or not, die back at the end of the rainy season. If the rainy season is unusually short, most of the plant's growth will have been covered-internode growth and is thus protected against the ensuing dry season.

The Kenyan collections, with the possible exception of *Heriz Smith s.n.*, are all from an 8 km section of the Nairobi–Magadi road. The Heriz Smith specimen might also have come from this area, as the name "Magadi" is often used in a general sense for the whole region of Lake Magadi and the dry, low altitude area to the north of it. If the Heriz Smith collection came instead from the vicinity of the town of Magadi, then the 600 m altitude, recorded with uncertainty above, would be correct.

The local distribution of *A. brenanianum* is not just an artifact of limited collections. The presence of a local endemic in this part of East Africa is consistent with the isolation of the very dry habitats of the region from equally dry conditions to the east and north by about 200 and 400 km, respectively. Other endemics in this area include species of *Turraea* (Meliaceae: Dale and Greenway, 1961) and *Barleria* (Acanthaceae: Napper and Agnew, 1974).

Aneilema brenanianum is most distinctive because of its persistent shoot bases covered by overlapping, papery sheaths. These shoot bases can become very stiff and semi-woody, with the consistency of dead grass culms. Overlapping sheaths, but without stiff shoots, have been observed only in *A. longirrhizum*, occasional plants of *A. hockii*, and seedlings of *A. rendlei*.

The aspect of the plants of *A. brenanianum* suggests affinities with *A. longicapsa*, *A. obbiadense*, *A. somaliense*, and *A. longirrhizum*. However, it differs from all of them in many floral characters, and their vegetative similarity is undoubtedly due to convergence.

The floral characters of *A. brenanianum* indicate that it is most closely related to *A. rendlei*, *A. taylorii*, and *A. usambarense*. All of them differ in lacking rhizomes and

tuberous roots, and in having petiolate leaves with long uniseriate hairs on both surfaces, a completely glabrous inflorescence, lilac or lavender flowers, narrower capsules, and smaller seeds. *Aneilema brenanianum* further differs from *A. rendlei*, its closest relative, in having smaller antherode lobes that always lack maroon spots, shorter medial staminode filaments and styles, longer lateral staminode filaments, less-dimorphic lateral stamen filaments, and generally fewer-seeded capsules. Its flowers also open considerably later than those of *A. rendlei*.

Section 4: *Somaliensia* Faden, new section

Pedicelli fructuum erecti ad recurvatos. Petalum medium redactum. Stamina lateralia filamentis basi libris, sigmoideis, glabris, infra medium geniculatis. Stamen medium anthera ephippiomorpha. Ovarium puberulum loculo dorsali plerumque bene formato et 1-ovulato, loculis ventralibus uterque 2(-4)-ovulatis. Capsulae puberulae.

TYPE SPECIES.—*Aneilema somaliense* C.B. Clarke.

Tuberous-rooted perennials with annual flowering shoots often disarticulating at the nodes at the end of the growing season (roots and habit of *A. grandibracteolatum* unknown). Leaves usually spirally arranged, sheaths mostly short, and laminae sessile.

Inflorescences terminal thyrses with mostly alternate cincinni. Inflorescence axis puberulous with uniform-length hook-hairs, lacking uniseriate hairs. Bracteoles generally membranous, cup-shaped, perfoliate or not, glandular near the apex.

Flowers perfect and staminate, or pistillate, perfect, and staminate. Fruiting pedicels erect or recurved to ~270°, persistent. Sepals puberulous with uniform-length hook-hairs. Petals glabrous, the medial reduced. Filament bases free. Medial staminode with antherode lobes sessile or shortly stipitate and connective slightly to not at all elongate. Lateral staminodes with filaments straight, then sharply decurved near the apex, antherode lobes stipitate. Lateral stamens with filaments S-shaped, geniculate (or probably so) below the middle, glabrous. Medial stamen with anther saddle-shaped. Ovary densely and uniformly eglandular- or glandular-puberulous, dorsal locule generally well developed and 1-ovulate, ventral locules each 2(-4)-ovulate, stigma usually small.

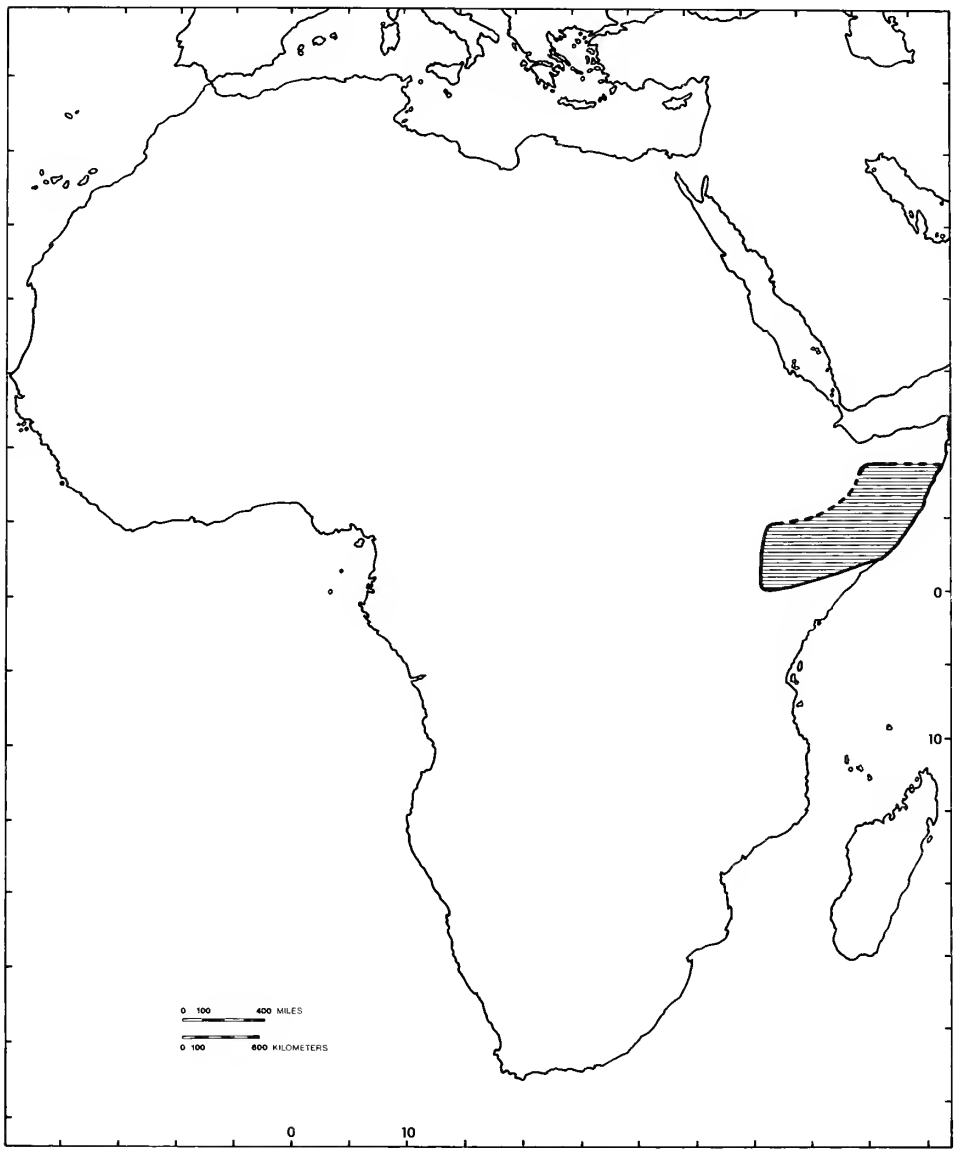
Capsules sessile or stipitate, dehiscent, bivalved, generally trilocular, lustrous, dorsal locule usually developed, 1-seeded or empty, ventral locules each 2(-4)-seeded. Seeds with a short or moderately long hilum, testa with pits and/or grooves on the dorsal surface radiating from the embryotega, farinose or not.

BASIC CHROMOSOME NUMBERS.—$x = 14, 16$.

DISTRIBUTION.—Somali Republic and E Ethiopia, S to central Kenya (Map 6).

Key to the Species of Section *Somaliensia*

1. Inflorescences composed of (8–)15–50 cincinni; cincinnus peduncles (2–)5–27 mm long.
   2. Bracteoles not perfoliate; capsules (5–)6–9 mm long, apex usually rounded to truncate; seeds 2–3(–4) per ventral locule, 1.6–2.7 mm long, white-farinose in the depressions . . . . . 1. *A. somaliense*
   2. Bracteoles usually perfoliate (rarely not); capsules (10.5–)12–17 mm long, apex ± rostrate; seeds 2 per ventral locule, 3.4–4.55 mm long, not farinose (mature seeds unknown in *A. obbiadense*).
      3. Bracteoles (2.5–)3–3.5 mm long, attached (2–)2.5–3.5 mm apart; cincinnus peduncles 7–13 mm long . . . . . 2. ***A. grandibracteolatum,*** new species
      3. Bracteoles (1.5–)1.9–3 mm long, attached 1.5–22 mm apart; cincinnus peduncles 10–27 mm long.
         4. Cincinnus peduncles 15–27 mm long; bracteoles attached 9–22 mm apart; lamina lanceolate to ovate, 1–2 cm wide . . . . . 3. *A. obbiadense*
         4. Cincinnus peduncles 10–20 mm long; bracteoles attached 1.5–7.5 mm apart; lamina usually linear-lanceolate and 0.35–0.8 cm wide, rarely lanceolate to lanceolate-elliptic and 0.8–1.9 cm wide . . . . . 4. ***A. longicapsa,*** new species
1. Inflorescences composed of 2–11(–13) cincinni; cincinnus peduncles (1.2–)1.5–5.5(–8.5) mm long . . . . . 5. *A. pusillum*



MAP 6.—Distribution of *Aneilema* section *Somaliensia*, new section.

DISCUSSION

The five species recognized in section *Somaliensia* are mostly inadequately known, with only *A. somaliense* and *A. pusillum* being represented by more than seven collections each. In particular, the relationships among *A. grandibracteolatum, A. obbiadense,* and *A. longicapsa,* collectively known from nine gatherings, need further investigation. Similarly, the treatment of *A. pusillum* as a species with four subspecies should be considered provisional, for it is based on only 14 collections.

The species in section *Somaliensia* fall into three distinct groups, the first consisting of *A. somaliense,* the second of *A. grandibracteolatum, A. obbiadense,* and *A. longicapsa,* and the third of *A. pusillum.* These groups are characterized mainly by inflorescence, capsule, and seed characters, which are given in the key and in the discussions under the individual species, and perhaps also by chromosome number. In view of our incomplete knowledge of most of these taxa, particularly of floral morphology, it would be premature to recognize subsections at this time.

1. *Aneilema somaliense* C.B. Clarke

Aneilema somaliense C.B. Clarke in Thiselton-Dyer, Fl. Trop. Africa, 8:69, 1901.—Chiovenda, Resultati Scientifici Missione Stefanini-Paoli Somalia Italiana, 1:167, 1916; Webbia 8:38, 1951.—Cufodontis, Bull. Jard. Bot. Natl. Belgique, 41, suppl., 1518, 1971. [Type: Ethiopia (Somaliland on label, see below), Harradigit, Mar (1885), *James & Thrupp s.n.* (K).]

Aneilema smithii C.B. Clarke in Thiselton-Dyer, Fl. Trop. Africa, 8:70, 1901.—Cufodontis, Bull. Jard. Bot. Natl. Belgique, 41, suppl., 1518, 1971. [Syntypes: Ethiopia, Lake Rudolf to Gondokoro, Jara, 23 Oct 1899, *Donaldson Smith s.n.* (BM, lectotype); Ethiopia, Lake Rudolf to Gondokoro, Anole, 21 Oct 1899, *Donaldson Smith s.n.* (BM).]

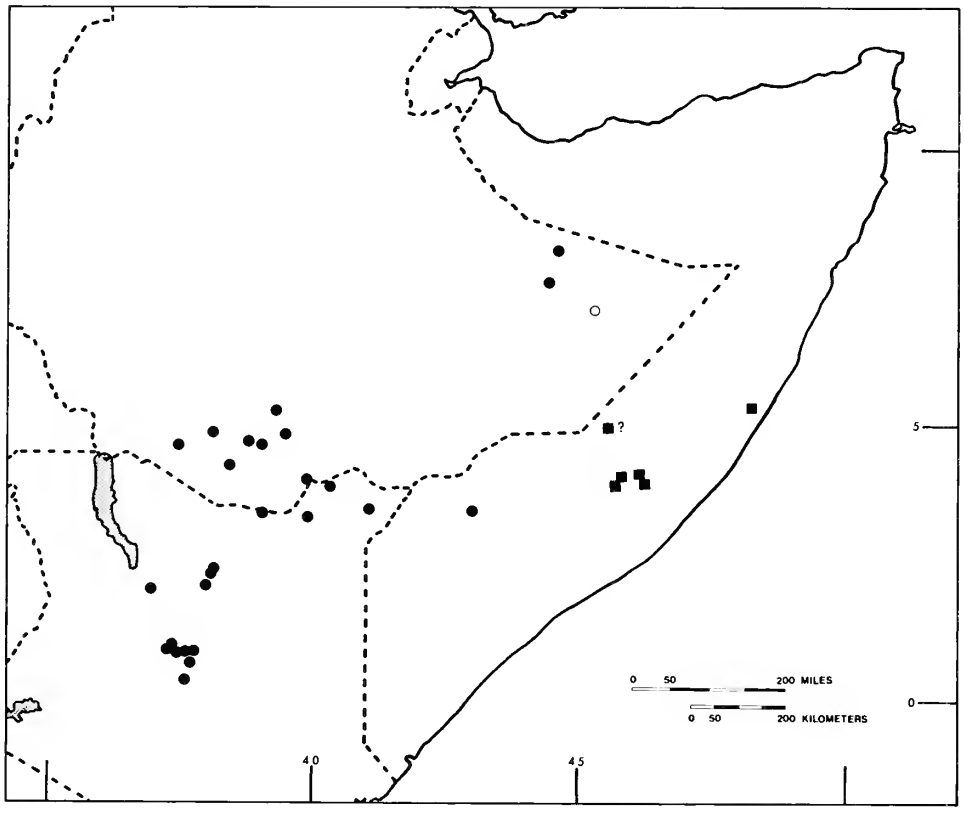
Aneilema tacazzeanum sensu Chiovenda, Missione Biol. Paese Borana, 4:305, 1939 [pro *Cufodontis 319*, non Hochstetter ex A. Richard (1850)].

Perennial herbs (habit types IVBI, IVB2, Figure 3). Roots tuberous, to 60 cm long, with distal fusiform to cylindrical tubers to 24 cm long. Perennial shoot bases subterranean, short, erect, sometimes a few connected, forming a short rhizome; flowering shoots annual, sparsely to profusely branched, erect to ascending, lower parts sometimes prostrate or looping on ground but not rooting at nodes, shoots disarticulating at base and nodes at end of growing season, 7.5–40 cm tall. Internodes (0.7–)1.5–8(–10) cm long, green, puberulous and rarely sparsely pilose. Leaves spirally arranged, sheaths 0.3–1(–1.5) cm long, puberulous and rarely sparsely pilose along the fused edge, ciliate at the apex, laminae sessile, lanceolate-elliptic to elliptic, ovate-elliptic or ovate, rarely broadly elliptic, (1.5–)2.5–7.5(–13) cm long, (1–)2–3.5(–5.5) cm wide, apex acuminate to acute, rarely obtuse or rounded, and then mucronate, base cuneate to rounded, rarely subcordate, margin planar to strongly undulate, scabrid and frequently ciliate, especially towards the base, both surfaces gray-green, lustrous, puberulous, usually with few to many, patent, uniseriate hairs less than 1 mm long, more numerous on abaxial surface (occasionally lacking on adaxial surface); midvein impressed on adaxial surface, prominent on abaxial surface.

Inflorescences thyrses (Plate 2*e*), terminal, moderately dense, ovoid to ellipsoid or cylindrical, (2–)3–9.5 cm long, (1.5–)2–4.5 cm wide, with (8–)17–40(–50) cincinni, alternate to subopposite or occasionally subverticillate, patent to ascending; occasionally a solitary cincinnus produced from the axil of the inflorescence bract. Peduncles 3–9 cm long, puberulous. Inflorescence bract medial to supramedial, commonly herbaceous and foliaceous, sometimes membranous and much reduced. Inflorescence axis puberulous. Cincinni up to 2.5 cm long and 8-flowered. Cincinnus bracts usually membranous, appressed to the cincinnus peduncles, ovate to lanceolate-ovate (rarely lanceolate), 1–2.5(–5) mm long, hooded and glandular apically, puberulous basally or entirely glabrous. Cincinnus peduncles shortest in lower cincinni, longest in middle cincinni, slightly reduced in uppermost cincinni, exceeding the cincinnus bracts, (2–)5–11(–13) mm long, greenish violet, puberulous. Cincinnus axes puberulous. Bracteoles attached 1–3.5(–4) mm apart, membranous, ovate, cup-shaped, amplexicaul but not perfoliate, 0.9–1.4(–1.7) mm long, with a prominent subapical gland, often puberulous, at least basally, rarely with a few uniseriate hairs along the margin towards the base, sometimes glabrous.

Flowers pistillate, perfect and staminate (Plate 2*f,g*), slightly fragrant, (7.5–)10–12.5(–17) mm wide. Pedicels 2.8–4.5(–5.5) mm long in flower, to 7 mm long in fruit, held in line with the cincinnus axis or slightly below in flower, erect to slightly recurved (rarely up to 180°) in fruit, persistent, glabrous, or occasionally with a few hook-hairs at the apex. Sepals with a prominent, green, subapical gland, puberulous; medial sepal ovate, (2–)2.8–3.5 mm long, 1.8–3.1 mm wide, gland inconspicuously bilobed; lateral sepals ovate-elliptic to lanceolate-ovate, (2–)2.4–3.1 mm long, 1.6–2.7 mm wide, gland inconspicuously bilobed or unlobed. Paired petals 4.8–9 mm long, 3.2–7 mm wide, limb ovate, 2.8–6 mm long, white to very pale lilac or pale blue (*Bally B10133*), apex rounded, usually slightly cucullate, claw 2–3 mm long, concolorous with limb, glabrous. Medial petal reflexed, ovate to lanceolate, elliptic or obovate-elliptic, 2.8–6 mm long, 1.6–4.5 mm wide, green medially with whitish margins, sometimes tinged with red apically. All filament bases free. Medial staminode with filament 1.3–2.7 mm long, yellow, sometimes purplish basally, antherode bilobed, yellow, lobes shortly stipitate, lanceolate, elliptic or broadly reniform, 0.4–1 mm long, connective scarcely elongate. Lateral staminodes with filaments 2.8–4.5 mm long, sharply decurved near the apex, purplish at base, yellow above, antherodes bilobed, yellow, lobes stipitate, obovate-cuneate to ellipsoid or suborbicular, 0.4–0.9 mm long, connective not elongate. Lateral stamens with filaments divergent in basal half, more strongly divergent apically (sometimes parallel or slightly convergent near the apex), 5–6.5 mm long, gently S-shaped, pendulous, glabrous, anthers elliptic to ovate, 0.6–1.3 mm long, 0.5–1 mm wide, pollen yellowish white. Medial stamen with filament 3.5–5 mm long, anther saddle-shaped, 0.9–1.1 mm long, 0.9–1 mm wide, connective broad, greenish white, pollen yellow or orange-yellow. Ovary sessile, oblong-elliptic, 0.9–2.5 mm long, 1.1–1.3 mm wide, densely and uniformly (except for a narrow V extending basally from the style base along the middorsal line) covered with spreading glandular hairs (Figure 42*c*), apex acute, dorsal locule represented by a prominent hump, empty or 1-ovulate, ventral locules (2–)3(–4)-ovulate; style 5.5–6.2 mm long, arcuate-decurved for most of its length, recurved near the apex, passing through the upper notch of the medial anther, held in floral midplane, sometimes with a few glandular hairs, like those of the ovary, at the base, stigma small, held in front of the anthers.

Capsules shortly stipitate, oblong-elliptic, bi- or rarely somewhat trivalved, bi- to trilocular, (5–)6–9 mm long, 3.2–4(–4.8) mm wide, stramineous to brown, lustrous, sparsely puberulous, apex rounded to truncate, occasionally emarginate or acute, valves persistent or occasionally dorsal valve tardily deciduous, dorsal locule occasionally obsolete but usually represented by a middorsal hump overlying the first and second pairs of seeds (from the base), empty or 1-seeded, ventral locules each 2–3(–4)-seeded. Seeds (Plate 5*g*) trapezoidal, rectangular, triangular or transversely ellipsoid, ventral apical rounded apically, ventral basal angular basally, 1.6–2.7 mm long (1.2–)1.3–1.6(–2) mm wide, hilum dark brown to dark gray, prominently raised within a groove, not at all to



MAP 7.—Distribution of *Aneilema somaliense* C.B. Clarke (solid circles), *A. grandibracteolatum* Faden, new species (open circle), and *A. longicapsa* Faden, new species (solid squares).

slightly extended onto apical and/or basal surfaces, testa pinkish brown to grayish tan or tan, interruptedly furrowed on the dorsal surface in a radiating pattern from the embryotega, some of the furrows continuing onto apical, basal and lateral surfaces, whitish farinose in all of the grooves and depressions and around the embryotega and hilum.

HABITAT.—*Acacia* or *Acacia-Commiphora* bushland or woodland, dwarf shrubland or degraded montane scrub, sometimes on rocky slopes; sandy, silty or loamy soils; generally growing in partial shade; 750–1700 m.

FLOWERING.—Flowering specimens have been seen from March–May, July, and October–December. In cultivation the flowers are open in the morning and fade in the early afternoon, but exact opening and fading times have not been determined.

CHROMOSOME NUMBER.—$n = 16$, $2n = 32$.

DISTRIBUTION.—E and S Ethiopia, S Somali Republic and N Kenya (Map 7).

SPECIMENS SEEN.—ETHIOPIA. HARAR: Ogaden Reserved Area, 37 mi E of Awareh, *Bally B10133* [*in CM22298*] (EA, K); Harradigit, Mar [1885], *James & Thrupp s.n.* (K). SIDAMO: 50 km S of Neghelli on Wachelli road, *Ash 823* (K); El Banno (Tertale), *Corradi 2196* (FT); Arero (Meta-Gafersa), *Cufodontis 319* (FT); Lake Rudolf to Gondokoro, Jara, 23 Oct 1899, *Donaldson Smith s.n.* (BM); Lake Rudolf to Gondokoro, Anole, 21 Oct 1899, *Donaldson Smith s.n.* (BM); Moyale area, 4°23′N, 38°25′E, *Everard in EA11456* (EA) [wrongly recorded as coming from Kenya on the label]; 10 km N of Neghelle, along road to Kebre Mengist, *Friis et al. 2670* (K); Old Airfield ~15 km NNE of Yavello, 4°59′N, 38°13′E, *Gilbert & Jefford 4559* (K); 46 km from turning to Mega on road from Negele, near Bulbula River, ~4°58′N, 39°37′E, *Thulin et al. 3539* (K).

SOMALI REPUBLIC. UPPER JUBA: Piana di El Ualàc, *Paoli 1085* (FT—2 sheets).

KENYA. MERU: Isiolo, *J. Adamson 599* (EA). NORTHERN FRONTIER: Mathews Range, Olkanto, *J. Adamson 42 in* [*Bally*] *B4343* (K); Gof Choba, 11 km N of Marsabit, 2°24.5′N, 38°03′E, *Carter & Stannard 652* (EA); 30 km S of Marsabit on Isiolo road, 2°08′N, 37°53′E, *Carter & Stannard 692* (EA); South Horr Valley, *Davey D79* (EA); 2 km WSW of Wamba, 0°57′N, 37°19′E, *Faden & Faden 74/923* (BR, EA, FT, K, MO, US); Matakweni Hill, 3 km WSW of Wamba, 0°57′N, 37°18′E, *Faden & Faden 74/939* (EA, FT, K, MO); Wamba–Isiolo road, near pass between Lekat and Olowa Werikoi Hills, 0°52′N, 37°24′E, *Faden & Faden 74/951* (EA, K, MO, PRE); Marsabit Mountain, *Gagal 556* (EA); Ol Lolokwe (Ol Doinyo Sabachi), E side of base, 0°52′N, 37°34′E, *Gilbert 5018* (EA); 5 km E of junction of Banissa and Derkali roads, ~3°55′N, 40°22′E, *Gilbert & Thulin 1452* (EA, F, US); 48 km on Ramu–El Wak

road, ~3°31′N, 41°00′E, *Gilbert & Thulin 1619A* (F); Subata Microwave Relay Station, NE part of Ol Lolokwe (Ol Doinyo Sabachi), 0°53′N, 37°34′E, *Gilbert et al. 5303* (EA); Dandu, 3°26′N, 39°54′E, *Gillett 12651* (K, PRE; EA, photo) and *12702* (B, BR, EA, K, S); Moyale, 3°32′N, 39°03′E, *Gillett 14032* (EA, K); [Marsabit District], Ngarunit fenced plot near outer airstrip, *Herlocker 757* (UNH); Archer's Post, Samburu Park, *Makin 233* (EA, K); Wamba, *Newbould 2957* (FT, K).

Discussion

There has been difficulty in localizing the types of *A. somaliense* and *A. smithii*. The type of the former has "Somaliland" written on the sheet, but the route followed by James and Thrupp, given in Chiovenda (1929) as "James 1885," shows that part of their journey was within the present boundaries of Ethiopia. The locality of the type, "Harradigit," is undoubtedly the same as "Harar Digit," for which Bally (personal communication) provided the coordinates 7°47′N, 44°27′E. This is close to the route shown by Chiovenda and is in Ethiopia, not the Somali Republic.

The Donaldson Smith collections that are the syntypes of *A. smithii* were recorded from "British East Africa, Lake Rudolph" by Clarke (1901). From the collector's account of his journey (Donaldson Smith, 1900) and the dates on the specimens, it has been determined that he was ENE of Moyale, near the present Kenya-Ethiopia border, not at Lake Rudolf (now Lake Turkana), as written on the labels, about the time he made these collections. Both specimens were probably collected in Ethiopia between Eimole (4°03′N, 40°12′E) in Kenya and El Der (3°52′30″N, 39°46′E) in Ethiopia.

The types of *A. somaliense* and *A. smithii* are very different looking vegetatively. The former, although consisting of only a single flowering shoot with the upper three leaves, is obviously a much larger plant with longer, proportionally narrower leaves than the latter. The only reproductive characters that appear to distinguish the types are the longer sepals and pedicels of *A. somaliense*. When a wider range of material was studied, it became apparent that these vegetative and reproductive differences were not taxonomically significant.

Aneilema somaliense and *A. smithii* were described in the same work (Clarke, 1901) and have not been combined previously. The former name has been selected because it suggests the general range of this species.

Aneilema somaliense is a very variable species. Most of that variation, however, is in the vegetative parts, and almost none of it is geographically based. The only exception is the collection *Paoli 1085,* the sole gathering from the Somali Republic, which is unusual in several of its shoots having broadly elliptic leaves that are sometimes rounded- or obtuse-mucronate at the apex. It is also unusual in some of its reproductive features: bracteoles frequently with uniseriate hairs on the margin towards the base and seeds radiately pitted instead of furrowed. In all other characters, *Paoli 1085* falls within the normal range of *A. somaliense*. There are at present insufficient grounds to separate it taxonomically.

Some variation observed in cultivated plants has not been found in field collected specimens. A cultivated plant of *Faden & Faden 74/923* produced small lateral shoots from many of its nodes. These shoots generated from their bases short, thick roots that perforated the leaf sheaths. When detached, these shoots could be grown as independent plants. This formation of plantlets has not been observed in specimens of *A. somaliense* nor in any other species of *Aneilema,* cultivated or wild.

The dimensions of many structures in the cultivated plants of *Faden & Faden 74/923* exceeded those of all other collections of this species. The measurements of the floral parts, capsule width, and seed length and width have been considered reasonable extensions of the range of variation and have been included in the description. The following have been omitted as being unlikely to occur in the field: inflorescences to 6 cm wide; cincinni all strongly ascending, up to 5 cm long and 12-flowered, with bracteoles attached up to 5 mm apart. Within a small geographic area *A. somaliense* can occupy quite diverse ecological sites. *Faden & Faden 74/939* was growing on a steep rocky slope beneath a massive granitic hill. It was found under shrubs of *Acalypha fruticosa* and an undescribed, spiny species of *Barleria* and was associated with the fern *Actiniopteris radiata*. Only one kilometer away, the same collectors' *74/923* was found in level *Acacia tortilis* subsp. *spirocarpa-A. brevispica* bushland growing in sandy soil with much bare ground between the trees and thicket clumps. These collectors' third collection in the same region (*74/951*) came from *Commiphora* bushland, in which the shrubs *Euphorbia cuneata* and *Boscia coriacea*, both absent from the other two localities, were common. In all three of these habitats, plants of *A. somaliense* occurred in protected spots under trees and shrubs.

The two annual flowering periods for *A. somaliense* coincide with the rainy seasons in its range. The Faden and Faden collections confirm that the flowering shoots die off completely during the long, dry season (June–September). It is unknown whether individual plants flower in both rainy seasons.

The relationships of *A. somaliense* have been difficult to assess. In overall appearance it shows similarities to some species in section *Brevibarbata*, e.g., *A. lanceolatum* and *A. welwitschii*. It differs from all of them in its glabrous stamen filaments and basic chromosome number. It also occurs entirely outside of the range of all species in that section. The similarities are probably due to convergence.

Aneilema somaliense also shares a number of features with species in section *Rendlei,* particularly *A. rendlei* and *A. brenanianum:* inflorescence form, scented flowers, glabrous filaments, small stigma, number of seeds per capsule locule, farinose testa, basic chromosome number, and ecology. However, those species have quite different habits, lacking distal tubers on their roots and having at least the basal part of the aerial shoots persisting during the dry season. They further

differ by lacking pistillate flowers, having a totally different androecial morphology, lacking conspicuous hairs on the ovaries and capsules, rarely having a well-developed dorsal locule in the capsule, and having seeds with a scrobiculate testa. The affinities of *A. somaliense* with section *Rendlei* species probably are not close.

As much through the absence of important discordant characters as through the presence of strong similarities, *A. somaliense* appears to be most closely related to the four other species placed in section *Somaliensia*. Although the data that have accumulated on these taxa since the decision to recognize section *Somaliensia* was made (Faden, 1975) have tended to demonstrate the more isolated position of *A. somaliense* within the section, important similarities have also been confirmed: tuberous roots, disarticulating, annual flowering shoots, short sheaths, sessile laminae, S-shaped, glabrous, lateral stamen filaments, saddle-shaped medial anther, well-developed dorsal locule in the ovary, small stigma, and radiately pitted or grooved testa. *Aneilema somaliense* differs from the other species in the section in having non-perfoliate bracteoles, glandular hairs on the ovary, more numerous ovules per ventral locule, basally angular ventral locule basal seeds, hilum in a groove that is not cut off at either end, and farinose testa.

2. *Aneilema grandibracteolatum* Faden, new species

Caules floriferi ad nodos disarticulati. Folia laminis lanceolatis vel lanceolato-ellipticis, 2.5–7.5 cm longis, 1–2.5 cm latis. Inflorescentiae thyrsi, 2–6 cm longi, 2–7 cm lati, cincinnis ~20–30 compositi. Bracteae cincinnorum (2.3–)3.5–5.8 mm longae. Cincinni pedunculis 7–13 mm longis, bracteolis (2–)2.5–3.5 distantibus. Bracteolae (2.5–)3–3.5 mm longae. Capsulae stipitatae, rostratae, (10.5–)12–14 mm longae, 3.5–3.8 mm latae, loculis ventralibus uterque 2-seminalibus. Semina 3.4–3.9 mm longa, 1.6–1.9 lata; testa aurantiaco-brunnea foveis sulcisque non profundis radiatis, granulis farinosis destituta.

TYPE.—Ethiopia (British Somaliland on label), between Walwal and Bulleh (Sirauw), 26 Nov 1944, *Glover & Gilliland 408* (K, holotype, photo F; EA, isotype).

Herbs, probably perennial (habit type unknown, probably IVB2, Figure 3). Roots unknown. Flowering shoots probably annual, erect to ascending, disarticulating at the base and nodes when dry, to 15 cm tall. Internodes 0.7–4 cm long, puberulous. Leaves spirally arranged, sheaths to 5 mm long, puberulous, sparsely ciliate (with short uniseriate hairs) or ciliolate with hook-hairs) at the apex, laminae sessile, lanceolate to lanceolate-elliptic, 2.5–7.5 cm long, 1–2.5 cm wide, apex acute to obtuse, base cuneate to rounded, margin usually undulate, scabrid with prickle hairs near the apex, otherwise beset with numerous hook-hairs, both surfaces puberulous, uniseriate hairs absent, except for some, poorly differentiated from prickle-hairs, midvein impressed on adaxial surface, prominent on abaxial.

Inflorescences thyrses, terminal, moderately dense to dense, ovoid to broadly ellipsoid, 2–6 cm long, 2–7 cm wide, with about 20–30 cincinni, alternate to subopposite, the lowermost often subverticillate, ascending to patent, the lowermost becoming declinate. Peduncles 1.8–5.2 cm long, puberulous, distance between inflorescence bract and lowest cincinnus 0.6–1.6 cm. Inflorescence bract supramedial to medial, foliaceous or reduced and bract-like. Inflorescence axis puberulous. Cincinni up to 3.5 cm long and 8-flowered. Cincinnus bracts scarious, appressed to the cincinnus peduncles, becoming reflexed with age, lanceolate to lanceolate-elliptic (2.3–)3.5–5.8 mm long, glandular near the apex, glabrous to sparsely puberulous. Cincinnus peduncles relatively uniform in length within the inflorescence, or the lowermost slightly reduced, exceeding the cincinnus bracts, 7–13 mm long, puberulous. Cincinnus axes puberulous. Bracteoles attached (2–)2.5–3.5 mm apart, sometimes slightly overlapping, herbaceous, eccentrically cup-shaped, perfoliate or sometimes not, (2.5–)3–3.5 mm long, to 2.5 mm high, inconspicuously glandular near the apex, puberulous at least towards the base.

Flowers probably perfect and staminate (only the latter seen). Pedicels 2.5–4.2(–5.7) mm long in flower, to 8.5 mm long in fruit, aligned with the cincinnus in flower, erect to recurved (to ~150°) in fruit, persistent, glabrous or sparsely puberulous at the apex. Sepals puberulous; medial sepal ~3.2 mm long, cucullate and glandular apically; lateral sepals elliptic to oblong-elliptic, ~3.5 mm long × 2.2 mm wide, inconspicuously glandular apically. Paired petals "pale blue," ~6–6.5 mm long, claw ~1.5 mm long. Medial petal reduced, ~4–4.5 mm long. All filament bases free. Medial staminode yellow, filament 0.7–1.5 mm long, slightly broadened apically, antherode bilobed, the lobes sessile, obovate to suborbicular, ~0.3 mm long × 0.4 mm wide, broadly or narrowly attached to the filament, connective slightly elongate. Lateral staminodes yellow, filaments ~4 mm long, antherodes bilobed, lobes stipitate, obovate- to suborbicular-cuneate, ~0.3 mm long × 0.25 mm wide, stalks ~0.15 mm long, attached at about right angles to the filament, connective not elongate. Lateral stamens with filaments ~8.5 mm long, geniculate below the middle, glabrous, anther elliptic, 1–1.5 mm long, ~1 mm wide. Medial stamen with filament ~5–5.5 mm long, anther saddle-shaped, 1.3–1.6 mm long. Ovary not seen but, extrapolating from capsule, probably stipitate, puberulous, apex acute, tapering into the style, dorsal locule 1-ovulate or empty, ventral locules each 2-ovulate; style (on young capsule) ~9 mm long, stigma small.

Capsules stipitate, oblong-elliptic, tapering at both ends, slightly falcate, dehiscent, bivalved, bi- to trilocular, (10.5–)12–14 mm long, 3.5–3.8 mm wide, stramineous, lustrous, evenly puberulous on both surfaces and all sutures, glandular hairs occasionally mixed with a few hook-hairs, apex ± rostrate, valves persistent, slightly spreading, dorsal locule obsolete or 1-seeded, ventral locules each 2-seeded, cells of the

capsule wall transversely elongate, in regular files. Seeds (Plate 5c) transversely elliptic, the apical ventral rounded apically, the basal ventral rounded basally, 3.4–3.9 mm long, 1.6–1.9 mm wide, hilum dark gray, much shorter than the seed, prominently raised within a groove, groove cut off apically and basally by ridges, with apical, basal and lateral edges crenate, embryotega pale pinkish gray, testa orange-brown, with very shallow pits and grooves radiating from the embryotega on the dorsal surface, the pits and grooves becoming deeper with distance from the embryotega, farinose granules lacking.

HABITAT.—"Open areas on sand" (*Glover & Gilliland 408*), probably in bushland.

FLOWERING.—The single collection from late November has flowers and mature capsules. It had probably been flowering for at least 3–4 weeks and was beginning to dry up, judging from the scarcity of large flower buds.

CHROMOSOME NUMBER.—Unknown.

DISTRIBUTION.—E Ethiopia (Map 7).

SPECIMENS SEEN.—ETHIOPIA. HARAR: Between Walwal and Bulleh (Sirauw), *Glover & Gilliland 408* (EA, K).

DISCUSSION

The Glover and Gilliland collection records the country as British Somaliland, but the coordinates for the two localities mentioned on the label indicate that the plants actually came from the Ogaden region of Ethiopia. The locality Sirauw (= Bulle Sirau) appears only on the EA specimen.

This species is clearly closely related to *A. obbiadense* and *A. longicapsa* because of its longly stipitate, rostrate, curved capsules and large, transversely elliptic seeds with a short hilum prominently raised within a groove that is cut off at one or both ends by ridges. *Aneilema grandibracteolatum* differs from *A. obbiadense* by its longer leaves and much smaller, denser inflorescences, from *A. longicapsa* by its broader leaves and smaller, more orange seeds, and from both by its shorter cincinnus peduncles and larger, less widely spaced bracteoles. Apparently it is also geographically isolated from them, based on the limited number of collections available. Floral characters, when they can be determined from living plants, will probably be decisive in establishing the final taxonomy of these species.

The large, pointed capsules in these three species and their northeastern African distributions, suggest a possible affinity with *A. gillettii* of section *Amelina*. However, that species has mostly subverticillate cincinni, bearded lateral stamen filaments, concolorous petals, sessile, more or less glabrous capsules with more seeds per locule, and farinose seeds of a different structure. The resemblance of the capsules is almost certainly due to convergence.

A recent collection from the Somali Republic, *Thulin 5667*, is somewhat intermediate between *A. grandibracteolatum* and *A. longicapsa*. It is discussed under the latter species.

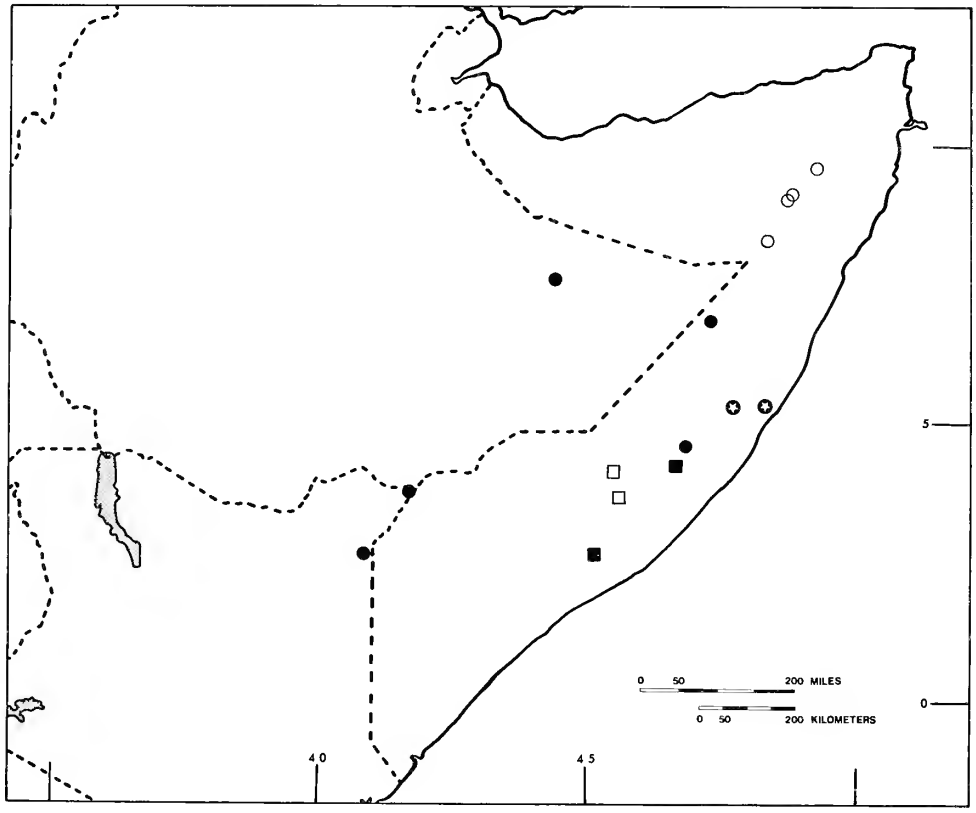
3. *Aneilema obbiadense* Chiovenda

Aneilema obbiadense Chiovenda ["Obbiadensis"], Pl. Novae Aethiopia, 10, 1928; Fl. Somala, 1:316, 1929.—Cufodontis, Bull. Jard. Bot. Natl. Belgique, 41, suppl., 1517, 1971. [Type: Somali Republic (Somalia centrale on label), Sultanato di Obbia, Tobungàb, 4 May 1924, *Puccioni & Stefanini 592* [*646*] (FT).]

Perennial herbs (habit type IVB2, Figure 3). Roots tuberous, ~4 mm thick at base, then abruptly narrowed and uniformly 2–3 mm thick for rest of their length, to 28 cm long (or longer?), distal swellings apparently absent but roots in specimens incomplete. Perennial shoots rhizomes, subterranean, moniliform, unbranched or sparsely branched, 7.5 cm long in specimen, each segment producing several roots and probably only one aerial shoot. Flowering shoots annual, erect, sparsely branched, disarticulating at base and nodes on drying. Internodes 1–2 cm long, puberulous. Leaves spirally arranged, sheaths often split to base or nearly so, to 0.5 cm long, puberulous, sparsely ciliolate with short uniseriate hairs or hook-hairs at the apex, laminae somewhat succulent, sessile, lanceolate to ovate, 2–5 cm long, 1–2 cm wide, apex acute, base rounded to broadly cuneate, margin undulate, scabrid with prickle-hairs near the apex and hook-hairs below, both surfaces puberulous, lacking uniseriate hairs.

Inflorescences thyrses, terminal, lax (or moderately lax), ovoid to subspherical, 4.5–11 cm long, 5.5–12(–~20) cm wide, with 15–21 cincinni, mostly alternate (or a few subopposite), except the lower, which are subverticillate, ascending, patent, or declinate. Peduncles 3–4 cm long, puberulous. Inflorescence bract medial, bract-like or foliaceous. Distance between inflorescence bract and lowest cincinnus 1–2 cm. Inflorescence axis puberulous with uniform-length hook-hairs, sometimes blue-tinged. Cincinni to 12 cm long and 6-flowered. Cincinnus bracts scarious, patent to ascending, ovate to ovate-elliptic, 2.5–3.5 mm long, glabrous or subglabrous. Cincinnus peduncles relatively uniform within the inflorescence, 15–27 mm long, sometimes blue-tinged, puberulous. Cincinnus axes puberulous with uniform-length hook-hairs, sometimes blue-tinged. Bracteoles attached 9–22 mm apart, scarious, cup-shaped, perfoliate, 2–2.7 mm long, 1.1–2 mm high, not clearly glandular, glabrous or with a few minute hairs near the base.

Flowers perfect and staminate. Pedicels 4.5–7 mm long in flower, to 10 mm long in fruit, aligned with the cincinnus axis in flower, strongly recurved (~180°–270°) in fruit, glabrous or sparsely puberulous. Sepals 3–6 mm long, glandular near the apex, but not very prominently so, (sparsely) puberulous with uniform-length hook-hairs. Paired petals lilac, 6 mm long and wide (fide type description). Medial petal narrow. All filament bases free. Medial staminode ~2.5 mm long, yellow, filament broadened apically, antherode (sometimes not developed) bilobed, lobes sessile, lanceolate-elliptic, ~1 mm long, asymmetric, attached near the base and parallel to filament, connective slightly elongate. Lateral staminodes ~5 mm long,



MAP 8.—Distribution of *Aneilema obbiadense* Chiovenda (solid circle with star), *A. pusillum* Chiovenda subsp. *pusillum* (solid squares), *A. pusillum* subsp. *gypsophilum* Faden, new subspecies (open circles), *A. pusillum* subsp. *thulinii* Faden, new subspecies (open squares), and *A. pusillum* subsp. *variabile* Faden, new subspecies (solid circles).

yellow, antherodes bilobed, lobes stipitate, obovate-cuneate. Lateral stamens with filaments S-shaped, ~10 mm long, glabrous, anthers (in bud) ovate. Medial stamen with anther saddle-shaped, subequal to the lateral anthers (in bud). Ovary sessile, densely and apparently uniformly puberulous, apex acute, tapering into the style, dorsal locule 1-ovulate, ventral locules each 2-ovulate, style 11–12 mm long, stigma small.

Submature capsule stipitate, fusiform, tapering at both ends, slightly falcate, dehiscent, bivalved, trilocular, 15 mm long, ~3.5 mm wide, stramineus, lustrous, uniformly puberulous, apex rostrate, dorsal locule 1-seeded, ventral locules each 2-seeded, cells of the capsule wall transversely elongate, in regular files. Immature seed (only one seen) transversely elliptic ~4.7 × 1.5 mm, hilum much shorter than the seed, raised within a groove, groove cut off apically or basally (but not both) by a ridge, testa apparently smooth.

HABITAT.—Stabilized, rocky sand dunes, and grassy, fixed dunes (with limestone exposures) dominated by prostrate bushes; ~50 m.

FLOWERING.—May.

CHROMOSOME NUMBER.—Unknown.

DISTRIBUTION.—Central Somali Republic (Map 8).

SPECIMENS SEEN.—SOMALI REPUBLIC. 18 Km SW of Obbia on road to Wisil, 5°17′N, 48°22′E, *Gillett et al. 22229* (EA, K, US); Tobungàb, *Puccioni & Stefanini 592* [*646*] (FT).

DISCUSSION

Some of the dimensions given here differ from those in Chiovenda's type description. Several of his measurements, e.g., leaf width and cincinnus bract length, appear to have been made inaccurately. Others seem to have come from a soaked bud and are therefore much too small, e.g., petal length and width. On the other hand, his measurement for sepal width is obviously too great, the sepals actually being much narrower than long. In the above description, Chiovenda's dimensions are given only when they accord with those that I have obtained or when they are the only dimensions available.

Based on the seeds in the capsule, the ovary should have one ovule in the dorsal locule and two in each ventral locule. I do not believe Chiovenda's description of the ovary as bilocular with each locule triovulate.

The most distinctive feature of this species is the very wide spacing of the bracteoles on the cincinni, greater than in any

other species in the genus. This character combined with the unusually long cincinnus peduncles gives the inflorescence a most distinctive facies. The disarticulating shoots are also unusual in the genus.

The rhizome and roots in *A. obbiadense* are very similar to those of *A. brenanianum*. That species differs in having much longer leaves with very long sheaths, the flowering shoots not disarticulating, the basal part persistent, a denser inflorescence with shorter cincinnus peduncles and internodes, the medial staminode with stipitate, reniform antherode lobes, the medial anther ellipsoid or ovoid with a very convex connective, the ovary glabrous with more numerous ovules per ventral locule. The floral differences show that the similarity in the subterranean parts of these two species is due to convergence and is not indicative of a close relationship. The true relationships of *A. obbiadense* are clearly with *A. grandibracteolatum* and *A. longicapsa* (see discussion under section *Somaliensia*).

4. *Aneilema longicapsa* Faden, new species

Aneilema obbiadense var. *angustifolium* Chiovenda ["angustifolia"], Pl. Novae Aethiopia, 10, 1928; Fl. Somala, 1:316, 1929. [Type: Somali Republic [Somalia centrale on label], Sultanato di Obbia, tra Scermàrca Hassàm e Tobungàb, 4 May 1924, *Puccioni & Stefanini 579* [*634*] (FT)].

Herbae perennes foliis spiraliter dispositis, laminis linearo-lanceolatis (ad lanceolato-ellipticas), 2–8 cm longis, 0.35–0.8(–1.9) cm latis. Inflorescentiae thyrsi ovoidei, 3.5–7.5 longi, 3–6.5(–9) cm lati, cincinnis (11–)13–36 compositi. Pedunculi cincinnorum 10–20 mm longi, bracteis longiores. Bracteolae 1.5–7.5 mm semotae. Sepala 3–5 mm longa, puberula. Petala 7–8.5 mm longa, 6.5–8 mm lata. Ovarium dense eglanduloso-puberulum, loculo dorsali 1-ovulato vel casso, loculis ventralibus 2-ovulatis. Capsulae stipitatae, rostratae, (12–)14–17 mm longae, loculis ventralibus plerumque uterque 2-seminalibus. Semina transverse elliptica ad oblongo-elliptica, 3.75–4.55 mm longa, 1.55–1.7 mm lata.

TYPE.—Somali Republic, Central Somalia, 17 km S of Mugakori, 3°57′N, 46°11′E, 6 June 1981, *Gillett & Beckett 23289* (K, holotype; EA, US, isotypes).

Perennial herbs (habit type IVA; Figure 3). Roots ± tuberous, 3–4 mm thick at base, then abruptly narrowed and 1.5–2 mm thick for rest of their length (possibly broadened distally in *Gillett et al. 22609*—US), to 28 cm long or longer. Aerial shoots annual, erect to ascending, sparsely branched, disarticulating at base when drying, to ~30 cm tall. Internodes 1–4.5 cm long, puberulous. Leaves spirally arranged, sheaths often split to the base or nearly so, to 0.5 cm long, puberulous, sparsely ciliate (with uniseriate hairs) or ciliolate with uniseriate hairs and/or hook-hairs at the apex, lamina sessile (to shortly petiolate in cultivation), linear-lanceolate (to lanceolate-elliptic), 2–8 cm long, 0.35–0.8(–1.9) cm wide, apex acuminate to acute, base cuneate (to rounded), margins planar, scabrid with prickle-hairs near the apex and hook-hairs below, both surfaces scabrous, puberulous, lacking uniseriate hairs.

Inflorescences thyrses, terminal, moderately dense to moderately lax, ovoid, 3.5–7.5 cm long, 3–6.5(–9) cm wide (to 10 cm wide in cultivation), with (11–)13–36 cincinni, mostly alternate, with the lower several subverticillate, ascending to patent. Peduncles 2–3.5(–5.5 in cultivation) cm long, puberulous. Inflorescence bract supramedial, usually foliaceous (occasionally bract-like). Distance between inflorescence bract and lowest cincinnus 0.5–1.3(–1.7) cm. Inflorescence axis puberulous with uniform hook-hairs, green tinged with blue. Cincinni to 5 cm long and 8-flowered (to 6 cm long and 9-flowered in cultivation). Cincinnus bracts scarious, ascending to reflexed, lanceolate to lanceolate-oblong or ovate-oblong, 2–4.5 mm long, not evidently glandular, glabrous or subglabrous. Cincinnus peduncles relatively uniform within the inflorescence (or the uppermost the longest), greatly exceeding the cincinnus bracts, 10–20 mm long, sometimes blue-tinged, puberulous. Cincinnus axis puberulous with uniform-length hook-hairs, sometimes blue-tinged. Bracteoles spaced 1.5–7.5 mm apart, scarious, eccentrically cup-shaped, perfoliate, (1.5–)1.9–3 mm long, 0.6–1.6 mm high, glandular subapically, sparsely puberulous basally or glabrous, margin usually erose basally.

Flowers perfect and staminate (Plate 2*h,l*), odorless, 15–18 mm wide. Pedicels 3.5–6.5 mm long in flower, to 9 mm long in fruit, ascending in flower, recurved in fruit at the base 120°–225° (mostly ~180°), green, glabrous or with a few hairs at the apex (occasionally puberulous on one side). Sepals convexo-concave, green, tinged with reddish purple basally, glandular near the apex but not prominently so, puberulous with uniform hook-hairs; medial sepal with a strongly cucullate apex, ovate to ovate-elliptic, 3–4.5 mm long, 2.1–2.5 mm wide; lateral sepals oblong-elliptic to ovate-elliptic, 3–5 mm long, 2–2.2 mm wide. Paired petals not overlapping, 7–8.5 mm long, 6.5–8 mm wide, limb ovate, 5.5–7 mm long, lilac (RHS color: 77C-D, *Gillett & Beckett 23289*), apex rounded, cucullate, base nearly symmetric, broadly cuneate; claw 1.5–2.5 mm long, glabrous. Medial petal lanceolate to lanceolate-elliptic or ovate-elliptic, 5–7 mm long, 2.5–3.3 mm wide, hyaline white faintly tinged with lilac in center, margins colorless. All filament bases free. Medial staminode 1.5–2 mm long, yellow, filament ~0.5–1 mm long, broadened apically, antherode bilobed, lobes sessile, oblong-elliptic to obovate, obliquely attached to filament, ~1–1.4 mm long, connective slightly to greatly elongate. Lateral staminodes yellow, filaments 4.5–6 mm long, antherodes bilobed, lobes stipitate, transversely elliptic to obovate, ~0.5 mm long, stalks 0.5–0.7 mm long, meeting filament at an acute angle, connective not elongate. Lateral stamens with filaments divergent, distinctly longer in staminate than perfect flowers but of similar curvature, 8.5–12 mm long, S-shaped, glabrous, white at base, pale pink above, anthers facing towards the flower base or towards the floral midplane and slightly forwards, ovate, 0.6–1.8 mm long, connective whitish, sutures blue-black, pollen dirty yellow. Medial stamen with filament 5–6.5 mm

long, arcuate ascending, white basally, pale pink medially, yellow apically, anther saddle-shaped, ovate, 1–1.8 mm long, connective yellow, pollen golden yellow (distinctly discolorous from lateral anther pollen). Ovary sessile, oblong-elliptic to elliptic, 2.5–3 mm long, ~1 mm wide, densely and uniformly covered with patent, colorless, eglandular hairs, apex acute, tapered into style, dorsal locule prominent or not, 1-ovulate or empty, ventral locules each 2-ovulate; style 9–12.5 mm long, arcuate-decurved then recurved, lilac, tapered at apex, stigma very slightly enlarged over the style apex, lilac.

Capsules stipitate, oblanceolate to oblong-oblanceolate, tapering at both ends, slightly curved, slightly constricted between the seeds, dehiscent, bivalved, bilocular (sometimes trilocular?), (12–)14–17 mm long (including stipe and beak), ~2.5–3 mm wide, chocolate brown or stramineous, lustrous, uniformly glandular-puberulous, apex rostrate, valves spreading less than 90°, cells of the capsule wall transversely elongate, in regular files. Seeds transversely elliptie to transversely oblong-elliptic, rounded to somewhat truncate at both ends (in 1-seeded locules) or rounded to somewhat truncate at one end and truncate at other end (in 2-seeded locules), 3.75–4.55 mm long, 1.55–1.7 mm wide, hilum dark brown, straight or slightly curved, much shorter than the seed, raised within a deep groove that is cut off at both ends by ridges, with margins of the groove crenate to lobed, testa light brown, scrobiculate, with the shallow pits and short grooves in more or less radiating lines from the embryotega, farinose granules lacking, embryotega tan.

HABITAT.—*Acacia-Commiphora* bushland on red, sandy soil, sometimes with limestone outcrops, also "elevated meadows"; 150–300 m.

FLOWERING.—Flowering specimens have been seen from May, June, and November. In greenhouse cultivation the flowers fade by mid morning.

CHROMOSOME NUMBER.—$2n = 64$.

DISTRIBUTION.—Central Somali Republic.

SPECIMENS SEEN.—SOMALI REPUBLIC. 17 km S of Mugakori, 3°57′N, 46°11′E, *Gillett & Beckett 23289* (EA, K, US); 5 km W of Mukwakori, 4°07′N, 46°05′E, *Gillett et al. 22609* (K, US); Sultanato di Obbia, tra Scermàrca, Hassàm e Tobungàb, *Puccioni & Stefanini 579* [*634*] (FT); 48 km on Maas-Bulo Burti road, ~4°06′N, 45°46′E, *Thulin & Warfa 4614* (K, UPS); 5–10 km along the road to Maas from the turning N of Bulo Burti, ~3°57′N, 45°36′E, *Thulin & Warfa 5341* (UPS).

DISCUSSION

When I first examined *Puccioni & Stefanini 579* [*634*], the holotype and then sole specimen of *A. obbiadense* var. *angustifolium*, I concluded that it could be encompassed within *A. obbiadense* without recognition as a distinct variety (Faden, 1975). The typical variety of the species was then also known from a single specimen. On the basis of more recent collections of both varieties, as well as the opinion of Gillett (in litt.), the only modern collector to have seen both in the field, I am now convinced that they represent distinct species. The differences in leaf shape, cincinnus peduncle length, and bracteole spacing given in the key appear consistent and give the plants quite a different facies. The species also seem to occur at different elevations. *Aneilema longicapsa* generally has shorter and less recurved fruiting pedicels than *A. obbiadense*. In all probability, additional characters will be found to separate these species when living material of *A. obbiadense* can be obtained and floral characters determined.

The recently collected *Thulin & Warfa 5341* has much broader leaves (0.8–1.9 cm wide) than the other collections (0.35–0.8 cm wide) and also differs from them in a few other details (some leaf bases rounded vs. all cuneate; lamina lanceolate to lanceolate-elliptic vs. lamina linear-lanceolate; capsules 12–14 mm vs. 14–17 mm long). In inflorescence characters, however, it fully agrees with the other specimens, and it has therefore been included in *A. longicapsa*.

Living material of *Gillett & Beckett 23289* was obtained by removing and planting seeds from the EA sheet. Although all four seeds that were planted germinated shortly after sowing in 1983, none of the plants survived dormancy, which is a common problem in cultivating species of section *Somaliensia*.

The dorsal locule in one of the three ovaries dissected in preserved flowers of *Gillett & Beckett 23289* contained an ovule. Therefore it is likely that capsules will be found that also contain a seed in this locule, although none has been encountered yet.

Another collection from the Somali Republic, *Thulin 5667* (US) (121 km SW of Dusa Mareb along road to Belet Huen), is similar to *Thulin & Warfa 5341*, but its leaves are still broader (to 2.5 cm wide) and its minimum dimension for cincinnus peduncle length (6 mm) falls outside the range for *A. longicapsa*, as circumscribed here. In both of these characters the specimen approaches *A. grandibracteolatum*.

Plants of *Thulin 5667* have been grown from seeds removed from the specimen, and they have been found to agree with previously cultivated plants of *A. longicapsa* (*Gillett & Beckett 23289*) in a number of significant characters of floral morphology (paired petal limbs hooded at apex; medial staminode filament broadened apically; lateral stamen filaments longer in staminate than in perfect flowers; pollen in lateral and medial anthers discolorous; ovary covered by relatively long, eglandular hairs) and in chromosome number ($2n = 64$). Because none of these characters is known in *A. grandibracteolatum*, the relationship of *Thulin 5667* to that species has not been clarified, whereas its closeness to *A. longicapsa* has been confirmed.

I believe that *Thulin 5667* will have to be included in *A. longicapsa* in the long run and that it likely will have to be separated at the subspecific level. I prefer to await further collections before taking that step. For this account, I have mapped it as *A. longicapsa* with a question mark (Map 7), but

I have omitted it from the exsiccatae above. If the specimen were formally included in *A. longicapsa*, some of the dimensions that would have to be changed in the species description, in addition to leaf width and cincinnus peduncle length cited above, are flowers to 20 mm wide; sepals to 5 mm long; paired petals to 12 mm long and 9.5 mm wide; medial petal to 8 mm long and 5 mm wide; lateral staminode filaments to 7 mm long; style to 13 mm long. Whether these dimensions will prove to fall within the normal range for *A. longicapsa* or perhaps will be useful is separating subspecies remains to be determined. It should be noted that the altitude range for *A. longicapsa* would have to be extended to 450 m if *Thulin 5667* were included in the species.

5. *Aneilema pusillum* Chiovenda

Aneilema pusillum Chiovenda, Resultati Scientifici Missione Stefanini-Paoli Somalia Italiana, 1:167, 1916.—Cufodontis, Bull. Jard. Bot. Natl. Belgique, 41, suppl., 1518, 1971. [Type: Somali Republic (Somalia Italiana on label), Praterie del Dafet fra Uanle Uein e Ildùc Uein, 19 Nov 1913, *Paoli 1277* (FT).]

Perennial herbs (habit types IVB2, IVB3, IVC2, Figures 1, 3; Plate 2*i*). Roots tuberous, fusiform, or uniformly thickened (subsp. *gypsophilum*), to 5 cm long and 0.7 cm thick, not stipitate. Rhizome absent, very short or somewhat elongate, to 2 cm long, old basal sheaths persistent or not. Flowering shoots annual, erect, unbranched or sparsely branched, 5–15(–18) cm tall. Internodes 1.3–4.5 cm long, glabrous or sparsely puberulous. Leaves spirally arranged or distichous, all cauline or mostly basal (subsp. *thulinii*), sheaths often split to the base, to ~0.8(–2) cm long, glabrous or sparsely puberulous, glabrous or sparsely ciliolate with hook-hairs at the apex, laminae moderately to very succulent when fresh, flat or conduplicate when drying, linear to semicircular in transverse section when fresh, usually ascending, sessile, linear or linear-oblong to linear-lanceolate, lanceolate-elliptic or ovate-elliptic, 2–9 cm long, 0.1–2 cm wide, apex acute to acuminate, base broadly cuneate to rounded, margin scabrid or not, usually with prickle-hairs towards the apex, glabrous or with hook-hairs below, sometimes ciliate basally, adaxial surface glabrous or nearly so, abaxial glabrous to puberulous with hook-hairs, uniseriate hairs lacking.

Inflorescences thyrses, terminal on main shoot and sometimes also on lateral shoots, moderately lax to moderately dense, narrowly ovoid to pyramidal, 1.5–6.5 cm long, (0.7–)1–3.5 cm wide, with (2–)6–10(–13) cincinni, alternate or occasionally subopposite, ascending to erect, the lowermost sometimes becoming patent or declinate. Peduncles 2–7(–8.5) cm long, glabrescent to puberulous. Inflorescence bract usually medial, generally foliaceous, rarely bract-like. Distance between inflorescence bract and lowest cincinnus 0.5–4 cm. Inflorescence axis often zigzag, sparsely to densely puberulous with uniform hook-hairs. Cincinni to 3 cm long and 8-flowered (or more in cultivation). Cincinnus bracts patent to reflexed or ascending, scarious (rarely the lowermost foliaceous), lanceolate to ovate, 1.2–7.5(–25) mm long, sometimes glandular near the apex, puberulous. Cincinnus peduncles relatively uniform within the inflorescences or the upper ones somewhat reduced (occasionally lowermost greatly exceeding the others), usually exceeding the cincinnus bracts, (1.2–)1.5–5.5(–8.5) mm long, puberulous or glabrous. Cincinnus axes puberulous. Bracteoles attached (0.6–)1–3.6(–6) mm apart, scarious, eccentrically cup-shaped, perfoliate, 1.1–3 mm long, 0.3–1.3 mm high (very rarely split to base), glandular near the apex, puberulous.

Flowers perfect and staminate, 6–9 mm wide (Plate 2*j,k*). Pedicels (1.5–)3–5 mm long in flower, to 6 mm long in fruit, aligned with the cincinnus axis in flower, erect or recurved 120°–270° in fruit, persistent, sparsely to densely puberulous. Sepals reflexed or not, green, sometimes tinged with purple or maroon, puberulous; medial sepal lanceolate to lanceolate-elliptic or ovate, 2–4 mm long, 1.3–2 mm wide, glandular or eglandular subapically; lateral sepals lanceolate-elliptic to ovate-elliptic, 2–4 mm long, 1.5–1.9 mm wide, not distinctly glandular. Paired petals 3–5.4 mm long, 2.5–4.5 mm wide, limb reflexed or not, ovate or ovate-elliptic to suborbicular (or obovate), ~3–4.4 mm long, pinkish red (RHS color: 51B-C, *Gillett et al. 22597*), pale lilac or blue (*Thulin & Warfa 4659*), apex rounded to obtuse, claw, (0.3–)0.7–1 mm long, yellow-green or whitish, glabrous. Medial petal narrowly lanceolate to lanceolate-ovate, ovate-elliptic or ovate, 2.5–4.5 mm long, 1.5–2 mm wide, greenish, tinged with pinkish red and pinkish red at apex, or flesh pink or white (sometimes tinged with pink), apex acute, sometimes recurved. All filament bases free. Medial staminode yellow, very variable in development, filament 0.45–1.4 mm long, antherode bilobed, lobes sessile to shortly stipitate, obovate-cuneate, transversely elliptic, transversely lanceolate or reniform, ~0.1–0.8 mm in diameter, connective slightly or not at all elongate. Lateral staminodes yellow, filaments 2–3.2 mm long, sharply decurved near the apex, antherodes bilobed, lobes stipitate, transversely ellipsoid or transversely lanceolate to ovoid, reniform or obovoid, 0.4–1.4 mm in diameter, connective not elongate. Lateral stamens with filaments strongly divergent at least above the middle, 2.8–6.5 mm long, S-shaped, glabrous, anthers elliptic to broadly elliptic, 0.8–1.5 mm long, connective pale gray or gray-green, pollen yellow or dirty yellow. Medial stamen with filament 2–5.2 mm long, anther shield-shaped to saddle-shaped, broadly elliptic to ovate, 0.5–1.4 mm long, connective yellow or white, pollen yellow or orange-yellow, discolorous from lateral anther pollen. Ovary sessile, elliptic or oblong-elliptic, 0.85–1.3 mm long, 0.65–1 mm wide, densely and uniformly puberulous, apex rounded to truncate, dorsal locule 1-ovulate, ventral locules each 2-ovulate; style 3.5–6.5 mm long, arcuate-decurved for most of its length, recurved near the apex, yellow in basal two-thirds, shading to lavender, lilac or maroon above, glabrous, stigma small or slightly enlarged.

Capsules sessile, elliptic to oblong-elliptic, dehiscent, bivalved, trilocular, 2.4–5 mm long, 1.5–2.5 mm wide,

stramineous (sometimes transversely streaked with brown) or brown, lustrous, puberulous with rather long hairs (to ~0.5 mm) with the apical cell sometimes becoming somewhat hooked (but true hook-hairs absent), apex acute to obtuse, truncate or emarginate, dorsal valve deciduous, dorsal locule prominent, 1-seeded or empty, ventral locules each 2-seeded (or less by abortion), cells of the capsule wall transversely elongate. Seeds (Plate 5*h*) transversely elliptic (dorsal locule seed) or subdeltate to ovate (ventral locule seeds), apical ventral rounded (or rarely acute) apically, basal ventral rounded basally, 1–1.9 mm long, 0.75–1.3 mm wide, hilum dark brown, much shorter than the seed, prominently raised within a groove, groove ± cut off apically and basally by ridges, with apical, basal and lateral edges crenate, testa tan or orange-tan, dorsal surface sulcate, (sulci radiating from the embryotega and becoming deeper towards the margins) or smooth with crenate margins, tan-farinose granules present or absent, if present, then confined to the embryotega and hilum.

Key to the Subspecies of *Aneilema pusillum*

1. Leaves all or mostly cauline at flowering time, lamina linear to linear-lanceolate, 0.1–0.8 cm wide.
   2. Plants not rhizomatous (or, if so, then other characters not as below); roots fusiform; plants growing on various substrates but usually not on gypsum.
      3. Lamina 0.1–0.3 cm wide; flowers coral red . . . . . *A. p.* subsp. ***pusillum***
      3. Lamina 0.3–0.8 cm wide; flowers pale lilac . . . . . *A. p.* subsp. ***variabile,*** new subspecies
   2. Plants rhizomatous; roots ± uniformly thickened, not fusiform; plants growing on gypsum . . . . . *A. p.* subsp. ***gyspsophilum,*** new subspecies
1. Leaves often mainly basal at flowering time, lamina lanceolate to ovate-lanceolate, the broadest 1–2 cm wide . . . . . *A. p.* subsp. ***thulinii,*** new subspecies

5a. *Aneilema pusillum* Chiovenda subsp. *pusillum*

HABITAT.—Open *Acacia-Commiphora* bushland on level red sand over limestone (*Gillett et al. 22597*); 135 m.

FLOWERING.— Flowering specimens have been seen from June and November. In greenhouse cultivation, flowers of *Gillett et al. 22597* opened between 1230–1400 hrs and remained open for about 4 hours.

CHROMOSOME NUMBER.—$n = 14$, $2n = 28$.

DISTRIBUTION.—Somali Republic (Map 8).

SPECIMENS SEEN.—SOMALI REPUBLIC. 8 km NE of Budbud, 4°15′N, 46°31′E, *Gillett et al. 22597* (US); Praterie del Dafet fra Uanle Uein [Uen] e Ildùc Uein [Ucn], *Paoli 1277* (FT).

5b. *Aneilema pusillum* Chiovenda subsp. *variabile* Faden, new subspecies

Ab subspecie typica foliis latioribus (0.3–0.8 cm latis, nec 0.1–0.3 cm) et floribus pallide lilacinis (nec roseis); ab subsp. *thulinii* foliis angustioribus semper omnibus caulinus tempore florendi differt.

TYPE.—Kenya, Mandera District, 6 km S of El Wak, ~2°46′N, 40°56′E, 30 Apr 1978, *Gilbert & Thulin 1251* (US, holotype; F, isotype).

HABITAT.—*Acacia-Commiphora* bushland and woodland and *Dichrostachys-Acacia* bushland, on limestone, among limestone rocks. or on level gypsum plain; 160–420 m.

FLOWERING.—Flowering specimens have been seen from April to June.

CHROMOSOME NUMBER.—Unknown.

DISTRIBUTION.—E Ethiopia, Somali Republic, and NE Kenya (Map 8).

SPECIMENS SEEN.—ETHIOPIA. HARAR: Harrodigit, communicated Apr 1885, *James & Thrupp s.n.* (K).

SOMALI REPUBLIC. 43 km E of Bahdo, 5°50′N, 47°08′E, *Gillett et al. 22399* (US); 12 km S of El Bur along road towards El Dere, ~4°37′N, 46°37′E, *Thulin & Warfa 4659* (UPS).

KENYA. NORTHERN FRONTIER: 6 km S of El Wak, ~2°46′N, 40°56′E, *Gilbert & Thulin 4659* (F, US); Accampamento di Bela [Beila] sul Daua, *Ruspoli & Riva 457* (*844*) (*438*) (FT).

5c. *Aneilema pusillum* Chiovenda subsp. *gypsophilum* Faden, new subspecies

Ab subspeciebus omnibus ceteris habitu rhizomifero radicibus plus minusve uniformiter incrassatis haud fusiformibus differt.

TYPE.—Somali Republic [Somaliland], Bihen, 2 Jun 1945, *Glover & Gilliland 1031* (K, holotype; EA, isotype).

HABITAT.—Gypsum hills and pediment; limestone pediment (*Beckett 1022*); 570–710 m.

FLOWERING.—Flowering specimens have been seen from April and June. Plants collected with old inflorescences in

November indicate flowering occurs in that month too.

CHROMOSOME NUMBER.—$2n = 28$.

DISTRIBUTION.—N Somali Republic (Map 8).

SPECIMENS SEEN.—SOMALI REPUBLIC. E of Gardo, 9°33′N, 49°07′E, *Beckett 1022* (EA); Bihen, *Glover & Gilliland 1031* (EA, K); 5 km SW of Halin along road to Gardo, 9°05′N, 48°40′E, *Thulin & Warfa 5423* (UPS, US); 8 km SW of Halin along road to Garoe, ~9°03′N, 48°46′E, *Thulin & Warfa 5395A* (US).

5d. *Aneilema pusillum* Chiovenda subsp. *thulinii* Faden, new subspecies

Ab subspecie typica foliis multo latioribus (ad 1–2 cm lata, nec 0.1–0.3 cm) saepe praecipue basalibus tempore florendi et floribus pallide lilacinis (nec roseis); ab subspecie *variabili* foliis latioribus (ad 1–2 cm lata, nec 0.3–0.8 cm) saepe praecipue basalibus tempore florendi differt.

TYPE.—Somali Republic, 4 km N of Bulo Burti, Gaala Karor, ~3°52′N, 45°34′E, 19 Nov 1985, *Thulin & Warfa 5320* (US, holotype; UPS, isotype).

HABITAT.—Limestone hills with *Acacia-Commiphora* bushland; 150–250 m.

FLOWERING.—Flowering specimens have been seen from May and November. Flowers of *Thulin & Warfa 5320* were observed in cultivation to open between 1130 and 1200 hrs.

CHROMOSOME NUMBER.—Unknown.

DISTRIBUTION.—C Somali Republic (Map 8).

SPECIMENS SEEN.—SOMALI REPUBLIC. 4 km N of Bulo Burti, Gaala Karor, ~3°52′N, 45°34′E, *Thulin & Warfa 4570* (UPS); same locality, *Thulin & Warfa 5320* (UPS, US); 62 km N of Bulo Burti along road to Belet Huen, *Thulin 5673* (US).

DISCUSSION

Recent field work, especially by Thulin and Warfa, has increased the total number of collections of *A. pusillum* from four to 14 since I first studied the species (Faden, 1975). At that time I suggested that three of those collections might require taxonomic segregation from the fourth (the type). The data obtained from the newer gatherings fully support that proposal, but some problems remain, largely due to the still incomplete information about these taxa.

Four subspecies are recognized here, but the number and taxonomic ranks of these infraspecific taxa may have to be reconsidered when more data have been obtained, particularly from living plants. One of the most distinctive subspecies is subsp. *gypsophilum*, which is characterized by a rhizomatous habit and non-fusiform, thick roots. It is also allopatric from the other subspecies. However, even subsp. *gypsophilum* is inadequately known. Capsules and seeds have not been collected, and the flowers have been studied only from pressed specimens. Specimens lacking bases and ecological notes and occurring outside the recorded range of subsp. *gypsophilum*, e.g., *James & Thrupp s.n.*, cannot be separated from subsp. *variabile* at present. They have been treated as the latter. Living plants of subsp. *gypsophilum* obtained for me by Mats Thulin yielded a chromosome number, but they died before flowering.

Plants of the typical subspecies are characterized by their gracile habit and very narrow leaves that are semicircular in cross-section. Living material was obtained from a still succulent base on one of the dried plants of *Gillett et al. 22597* that was received as a gift for determination. The red flower color reported by these collectors and confirmed from the living plant is unique in the genus, but whether it occurs in other populations of subsp. *pusillum* remains to be determined.

When I first received a specimen of subsp. *thulinii* (*Thulin & Warfa 4570*), I was convinced that it represented a new species related to *A. pusillum*. Its very broad leaves which were mainly basal gave the plant a very distinctive facies. At my request, Mats Thulin later collected for me living plants from the same population as his earlier gathering and from another population. Unlike the first collection, the new ones had capsules and seeds. Some plants grown from seeds exhibited the rosette habit of the original specimen. Others produced mainly caulescent leaves, as in the other collections of *A. pusillum*. The capsules and seeds also firmly placed the new collections in *A. pusillum*, but the very broad leaves and the tendency for them to be basal indicated that these plants needed to be segregated taxonomically.

Subspecies *thulinii* is named in honor of Dr. Mats Thulin, whose collections of this and other *Aneilema* taxa from Somalia, Ethiopia, and Kenya have greatly aided my research on the genus.

The most widespread subspecies—the only one not confined to the Somali Republic—and also the most poorly defined is subsp. *variabile*. Its leaves are always broader than those of subsp. *pusillum* but narrower than those of subsp. *thulinii*, with both of which it shares the character of fusiform roots. Its leaves vary from flat, as in subsp. *thulinii*, to conduplicate, as in at least some plants of subsp. *gypsophilum*. It is not certain whether subspecies *variabile* exhibits any unique characters; it is presently defined by the absence of the distinct features that define the other subspecies. *Thulin & Warfa 4659* has a distinct rhizome, but it is more elongate than that of subsp. *gypsophilum* and the roots are fusiform, so the collection has been placed in subsp. *variabile*.

Despite all of the variation, *Aneilema pusillum* is a very distinctive species because of the plants' small size, very succulent leaves, few-branched inflorescences, small, late-opening flowers, deciduous dorsal capsule valves, seeds with a short hilum completely surrounded by a crenate-margined ridge, and unique chromosome number for the genus.

Section 5: *Lamprodithyros* (Hasskarl) C.B. Clarke

Aneilema section *Lamprodithyros* (Hasskarl) C.B. Clarke in De Candolle, Monogr. Phan., 3:196, 1881, p.p.; in Thiselton-Dyer, Fl. Trop. Africa, 8:62, 1901, p.p.—Morton, J. Linn. Soc., Bot., 59:439, 1966, p.p.

Lamprodithyros Hasskarl, Flora, 46:388, 1863, pro gen.; in Peters, Naturwiss. Reise Mossambique, Bot., 529, 1864. [Lectotype: *Lamprodithyros petersii* Hasskarl (= *Aneilema petersii* (Hasskarl) C.B. Clarke).]

Aneilema section *Pseudo-axillares* C.B. Clarke in Thiselton-Dyer, Fl. Trop. Africa, 8:63, 1901, in clavi.— Morton, J. Linn. Soc., Bot., 59:439, 1966, pro syn. [Lectotype: *Aneilema clarkei* Rendle.]

Ballya Brenan, Kew Bull., 19:63, 1964, pro. gen. [Type: *Ballya zebrina* (Chiovenda) Brenan (= *Aneilema zebrinum* Chiovenda).]

Perennial or annual herbs with fibrous roots and spirally arranged or distichous leaves.

Inflorescences terminal (and often axillary) thyrses, rarely all axillary, sometimes all reduced to single cincinni. Inflorescence axis (when present) puberulous with hook-hairs of uniform length (rarely glabrous). Cincinni elongate or contracted. Bracteoles membranous to herbaceous, usually cup-shaped, perfoliate, glandular, or eglandular subapically, occasionally also with small glands along the margin.

Flowers perfect and staminate (rarely all perfect) (Plates 2*m–p*, 3, 4*a–h*), odorless. Pedicels erect in fruit or, more commonly, recurved 120°–270°(–360°), persistent, usually puberulous at least at the apex (occasionally glabrous). Sepals glandular subapically or occasionally apparently eglandular; hook-hairs, when present, of uniform length. Petals subequal, usually concolorous, white to lilac or lavender, glabrous; medial petal cup-, boat-, or slipper-shaped (Figures 23, 24), often retaining the lateral stamens when the flower opens. Filament bases of the stamens fused, frequently also fused to the lateral staminode bases for a shorter distance (Figures 26–28). Staminodes with yellow, bilobed antherodes; medial staminode absent or much shorter than the lateral staminodes, antherode, when present, generally equal to or smaller than those of the lateral staminodes. Lateral staminodes with filaments nearly straight, then usually sharply decurved (occasionally recurved) near the apex. Lateral stamens with filaments ± S-shaped, commonly sharply recurved above the middle, glabrous. Medial stamen with filament generally yellow apically, anther larger than the lateral anthers, saddle-shaped, connective and pollen usually yellow (rarely white). Ovary sessile to stipitate, ± densely and uniformly covered with patent, glandular hairs, sometimes mixed with few to many hook-hairs, dorsal locule prominent, usually 1-ovulate, ventral locules each 2-(rarely 1- or 3–4-)ovulate; style arcuate-decurved, usually recurved towards the apex, also commonly curved laterally out of the floral midplane, stigma capitate.

Capsules usually stipitate or substipitate (Figure 35), usually dehiscent (rarely indehiscent), bivalved (rarely partially trivalved), usually trilocular, lustrous, generally puberulous, apex commonly emarginate (rarely obtuse, rounded, or truncate), valves persistent or dorsal valve deciduous, dorsal locule usually prominent, commonly 1-seeded, ventral locules each 2-(or, by abortion, 0–1-)seeded (rarely 3–4-seeded), cells of the capsule wall usually transversely elongate (occasionally irregular). Seeds of the dorsal and ventral locules commonly dimorphic, that of the ventral locule often differing in shape, size (particularly length and thickness), testa color and markings, presence or absence or abundance of farinose granules and color of the embryotega (Plate 6*a,f,g);* dorsal locule seeds flat or convexo-planar, usually elliptic, oblong-elliptic or ovate-elliptic in outline; ventral locule seeds usually ovate to triangular or trapezoidal, apical seed rounded to obtuse or acute apically, basal seed usually angular basally, hilum usually in a groove, testa generally shallowly scrobiculate or reticulate, farinose granules usually sparse (except around the hilum), occasionally absent, hypha-like filaments sometimes present among the farinose granules.

BASIC CHROMOSOME NUMBER.—$x = 13$.

DISTRIBUTION.—Red Sea Hills of NE Sudan and S Arabian Peninsula S to Zimbabwe, Swaziland, and South Africa (N Transvaal, N Natal) (Map 9).

Key to the Species of Section *Lamprodithyros*

1. Some or all inflorescences terminal thyrses with a distinct inflorescence axis; cincinni elongate.
   2. Pedicels glabrous, or with a few hairs at apex, mostly erect in fruit; bracteoles cup-shaped, prominently glandular along the margin, glabrous; sepals glabrous; capsules sometimes with more than 2 (up to 4) seeds per ventral locule.
      3. Plants annual; leaf margins usually only scabrid, occasionally also sparsely ciliolate; capsules (2.25–)3.3–4.5(–4.9) mm wide; dorsal locule seed 2.7–3.45 mm long, 1.95–2.1 mm wide, 1.25–1.5 mm thick; ventral locule seeds (1.4–)1.7–2.2(–2.5) mm wide; (1.1–)1.2–1.45(–1.55) mm thick . . . . . 5. ***A. forskalii***
      3. Plants perennial; leaf margins scabrid and ciliate; capsules (2.3–) 2.8–3.6 (–3.7) mm wide; dorsal locule seed 2.15–2.85 mm long, 1.5–1.7 mm wide, 1–1.2 mm thick; ventral locule seeds 1.55–1.9(–2) mm wide, 1–1.25 mm thick . . . . . 4. ***A. sebitense,*** new species

2. Pedicels puberulous above the middle or occasionally only at apex, mostly recurved 180° or more in fruit; bracteoles various; sepals usually puberulous, rarely nearly glabrous; capsules with never more than 2 seeds per ventral locule.
   4. Medial sepal with marginal (as well as subterminal) glands; fruiting pedicels recurved 180°–270°(–360°); bracteoles with marginal glands; medial staminode lacking or vestigial and lacking an antherode.
      5. Inflorescences with 10–21 cincinni; bracteoles attached (1.5–)2–3(–3.3) mm apart, glabrous; sepals glabrous or subglabrous; capsules 3.5–4 mm long . . . . . 7. *A. benadirense*
      5. Inflorescences with up to 8 cincinni; bracteoles attached 1–2(–2.5) mm apart, puberulous at least basally; sepals puberulous; capsules (2.4–)2.7–3(–3.4) mm long . . . . . 8. *A. tanaense*
   4. Medial sepal with only a subterminal gland; fruiting pedicels mostly recurved ~180°; bracteoles lacking marginal glands (except *A. recurvatum*); medial staminode with an antherode.
      6. Pedicels puberulous only at apex; upper sepal glabrous; bracteoles glabrous, with small, inconspicuous marginal glands; capsules mostly 3.5–5 mm long × 2–2.5 mm wide . . . . . 3. *A. recurvatum,* new species
      6. Pedicels usually puberulous in upper half, rarely only at apex; all sepals puberulous; bracteoles puberulous (rarely subglabrous), lacking marginal glands (margin sometimes thickened in *A. indehiscens* but not distinctly glandular); capsules mostly 4.5–7.5 mm long × 2.3–5 mm wide.
         7. Lamina lacking long, uniseriate hairs on the adaxial surface; bracteoles symmetrically to asymmetrically cup-shaped, lacking long, uniseriate hairs; Arabian Peninsula . . . . . 6. *A. woodii,* new species
         7. Lamina with long, uniseriate hairs on both surfaces; bracteoles asymmetrically cup-shaped or not cup-shaped, commonly with 1-several long, uniseriate hairs towards the base; Africa.
            8. Bracteoles not cup-shaped, although sometimes shortly perfoliate basally; lateral stamen filaments crossing; capsules (2.4–)3.3–5(–5.5) mm wide, pale gray or brown, peppered with numerous, small, dark brown and/or black spots, dorsal valve deciduous; dorsal and ventral locule seeds strongly dimorphic, differing in shape, size, testa surface and color, and embryotega color; dorsal locule seed hemispherical, humpbacked towards the capsule apex, 2–2.6(–3.1) mm wide, 2.3–3.4 mm long, 1.6–2.1 mm thick, testa smooth . . . . . 1. *A. petersii*
            8. Bracteoles cup-shaped, usually some or all perfoliate; lateral stamen filaments not crossing; capsules (1.9–)2.3–3(–3.4) mm wide, chestnut brown or mottled dark and light brown or gray-brown, dorsal valve usually persistent; dorsal and ventral locule seeds scarcely dimorphic, differing only in shape and length, dorsal locule seed ± flat, 1.35–1.65(–1.9) mm wide, 2–2.9 mm long, 0.65–1 mm thick, testa shallowly scrobiculate . . . . . 2. *A. indehiscens*

1. All inflorescences composed of solitary or clustered, usually abbreviated cincinni, always lacking an inflorescence axis or all inflorescences axillary.
   9. Some or all inflorescences terminal on the main and major lateral shoots; flowers (9–)10–15(–20) mm wide; pedicels (4–)5.5–11(–13) mm long, recurved in fruit 180°–270°(–360°);capsules dehiscent, apex truncate to emarginate, dorsal locule very prominent; ventral locule seeds 0.8–1.2 mm thick, testa usually shallowly scrobiculate.
      10. Inflorescences consisting of 1–8 fasciculate cincinni, not enclosed in a pair of leafy bracts; fruiting pedicels recurved ± uniformly for their entire length; medial staminode absent or vestigial and lacking an antherode.

11. Bracteoles attached 1-2(-2.5) mm apart, with small marginal glands; medial sepal generally with marginal glands; lateral stamen pollen yellow . . . . . 8. ***A. tanaense***
11. Bracteoles attached 0.2-1(-1.4) mm apart, lacking marginal glands; medial sepal lacking marginal glands; lateral stamen pollen white . . . . . 9. ***A. calceolus***
10. Inflorescences consisting of solitary cincinni partially enclosed in a pair of leafy bracts; fruiting pedicels recurved only at the apex; medial staminode generally with an antherode.
12. Laminae petiolate, bases symmetric; internodes not swollen; capsules 3.6-4.5(-5) mm long; dorsal locule seed 1.65-2.15 mm long, 1.35-1.55 mm wide.
13. Flowers (12.5-)15-20 mm wide; pedicels puberulous apically; sepals glandular subapically; medial anther yellow, with yellow pollen; capsules 2.3-3 mm wide; testa of dorsal locule seeds light brown . . . . . 10. ***A. clarkei***
13. Flowers 10.5-14(-15.5) mm wide; pedicels pilose-puberulous apically; sepals apparently eglandular; medial anther white with white pollen; capsules 1.95-2.1(-2.55) mm wide; testa of dorsal locule seeds tan, orange-buff or orange-brown, usually heavily spotted and striped with dark brown . . . . . 11. ***A. lamuense,*** new species
12. Laminae sessile, bases asymmetric; internodes commonly swollen; capsules (2.8-)3.2-3.7(-4.3) mm long; dorsal locule seed 1.35-1.55 mm long, 1.2-1.25 mm wide . . . . . 12. ***A. succulentum,*** new species
9. All inflorescences axillary; flowers 7-10 mm wide: pedicels (0.5-)1.5-5 mm long, erect or slightly further recurved in fruit; capsules indehiscent or partially dehiscent, apex obtuse to rounded or truncate, dorsal locule a low hump; ventral locule seeds 0.5-0.6 mm thick, testa shallowly reticulate . . 13. ***A. zebrinum***

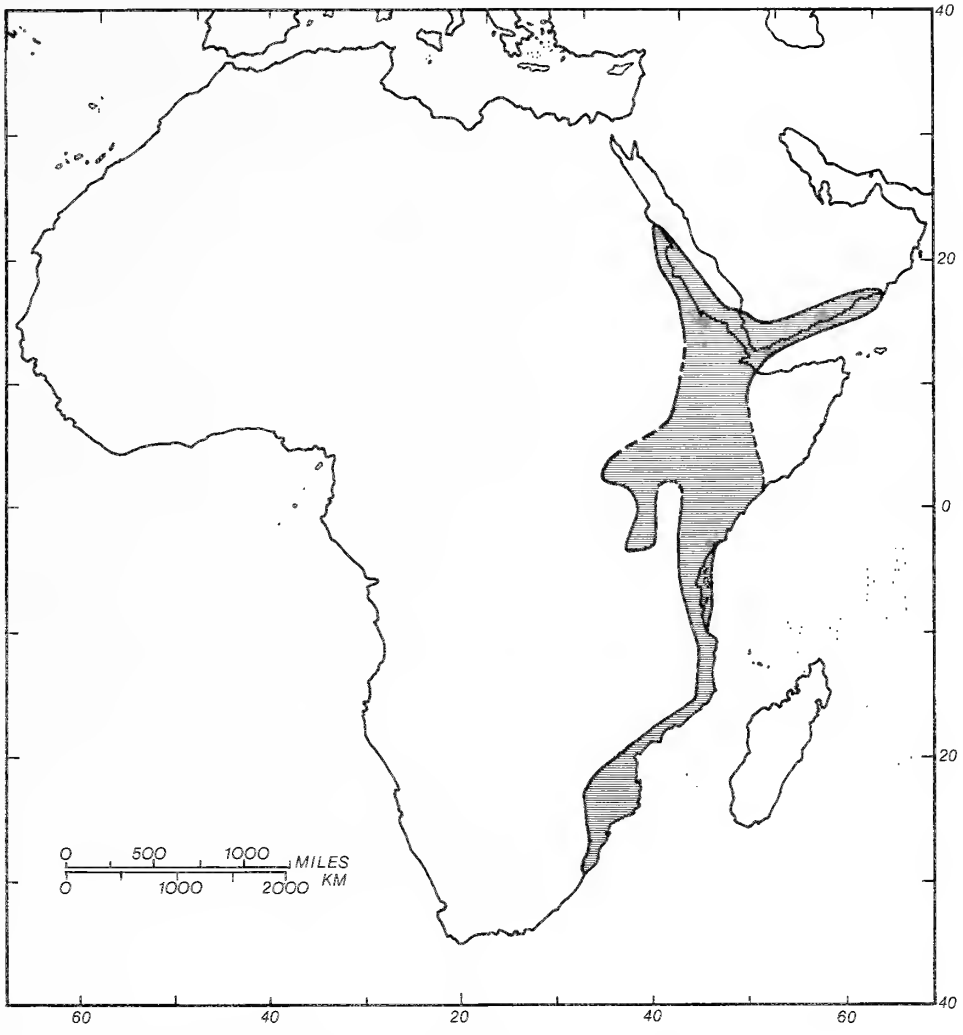
The lectotypification of *Lamprodithyros* Hasskarl by *L. petersii* requires some explanation because Hasskarl's circumscription (Hasskarl, 1863, 1864a) of the genus is equivalent to *Aneilema* as a whole in the sense used here, rather than to a section of it. Along with his description of the genus, Hasskarl (1863) published ten combinations in *Lamprodithyros*, two of which, *L. radicans* and *L. stenorrhachys*, are based on manuscript names and are nomina nuda. Of the remaining eight, five (*L. schomburgkianus* (Kunth) Hasskarl, *L. petersii* Hasskarl, *L. dregeanus* (Kunth) Hasskarl, *L. tacazzeanus* (Hochstetter ex A. Richard) Hasskarl, and *L. beniniensis* (P. de Beauvois) Hasskarl) belong to *Aneilema* in the present sense.

The description of *Lamprodithyros* and accompanying notes do not necessitate the selection of any particular species as the lectotype. However, Hasskarl (1863) included diagnoses for *L. petersii* and *L. tacazzeanus*—these were later amplified into lengthy descriptions (Hasskarl, 1864a)—but not for the others. It is reasonable to choose one of the two species that Hasskarl studied in detail as the type species of *Lamprodithyros*. *Lamprodithyros petersii* has been selected because (1) the type still exists in the Berlin Herbarium, and this species was not confused with any other by Hasskarl, and (2) Hasskarl's diagnosis and description of *L. tacazzeanus* were based on a Mozambique collection, but true *Aneilema tacazzeanum* Hochstetter ex A. Richard (= *A. forskalii* Kunth), does not occur south of Ethiopia, and the specimen that Hasskarl studied (fragment seen at L) was *A. nyasense* C.B. Clarke.

Clarke's section *Pseudo-axillares* includes three species, *A. pedunculosum* C.B. Clarke, *A. clarkei* Rendle, and *A. taylorii* C.B. Clarke, which are here placed in three different sections. Section *Pseudo-axillares* was based on the presence of axillary inflorescence-shoots, the "cyme-branches" of Clarke (1901). Because these occur in all sections of the genus, section *Pseudo-axillares*, as construed by Clarke, is clearly unnatural. Clarke's description does not favor typification of the section by any particular species. *Aneilema clarkei* conforms with the description and is here chosen as the lectotype. The resultant synonymy of section *Pseudo-axillares* with section *Lamprodithyros* agrees with the treatment of Morton (1966).

The genus *Ballya* was based on the single species *A. zebrinum* (Brenan, 1964). Supposed anatomical differences between *Ballya* and *Aneilema* were reported by Tomlinson (1966). Brenan's chief character for recognizing *Ballya* was an artifact of cultivation, and Tomlinson did not have available other species of section *Lamprodithyros* that are anatomically similar to *A. zebrinum*. Further details are given in the discussion under *A. zebrinum*.

Section *Lamprodithyros* is very natural as evidenced by the



MAP 9.—Distribution of *Aneilema* section *Lamprodithyros*.

great similarity in floral and capsular morphology among the species, the difficulty in separating many of the taxa from incomplete dried specimens, and the single basic chromosome number. The large, cup-, boat-, or slipper-shaped medial petal, which is usually the same (or nearly the same) color as the paired petals and, in many species, retains the lateral stamens for some time after the flower opens (see Faden, 1983b), is the most distinctive feature. Also very characteristic are the fused stamen filament bases and the trilocular capsule in which the dorsal and ventral locule seeds are commonly strongly dimorphic. When the seeds are very dimorphic, the dorsal valve of the capsule is usually deciduous.

Within section *Lamprodithyros* there are several closely related groups of species: *A. sebitense, A. forskalii,* and *A. woodii; A. benadirense, A. tanaense,* and *A. calceolus;* and *A. clarkei, A. lamuense,* and *A. succulentum. Aneilema petersii* and *A. recurvatum* also seem to be closely related to each other, and *A. indehiscens* may have arisen as an allotetraploid hybrid between them. *Aneilema zebrinum* seems to have been an offshoot of the *A. clarkei* species group. The relationships among the various species groups to one another remains to be determined.

1. *Aneilema petersii* (Hasskarl) C.B. Clarke

Aneilema petersii (Hasskarl) C.B. Clarke in De Candolle, Monogr. Phan., 3:225, 1881, p.p.; in Thiselton-Dyer, Fl. Trop. Africa, 8:70, 1901, p.p.—Durand and Schinz, Conspect. Fl. Africae, 5:131, 1895, p.p.—Schumann in Engler, Pflanzenwelt Ost-Afrikas C, 136, 1895, p.p.—Brenan, Kew Bull., 7:195, 1952.—Faden in Agnew, Upland Kenya Wild Fl., 666, 1974.

Lamprodithyros petersii Hasskarl, Flora, 46:389, 1863; in Peters, Naturwiss. Reise Mossambique, Bot., 529, 1864. [Type: Mozambique (without locality), Festland, an feuchten Orten (undated)] *Peters s.n.* (B, fragment L).]

Aneilema tetraspermum K. Schumann in Engler, Pflanzenwelt Ost-Afrikas C, 136, 1895. [Syntypes: Tanzania, Tanga, Feb 1893, *Volkens 175* (B, destroyed; K, lectotype; BM, G, isolectotypes); *Stuhlmann 6062* and *6458* (both B, both destroyed).]

Aneilema leptospermum K. Schumann ["leptasperma"], in sched. [*Volkens 175*].

Aneilema sacleuxii Hua, Bull. Mus. Hist. Nat. (Paris), 1:121, 1895.—Clarke in Thiselton-Dyer, Fl. Trop. Africa, 8:74, 1901. [Type: Zanzibar, bord de la mer, Apr 1890, *Sacleux 1142* (P; photo K) (cited as *"Sacleux 1192"* by Brenan, Kew Bull., 7:195, 1952).]

Aneilema chrysanthum K. Schumann, Bot. Jahrb. Syst., 33:1903. [Type: Tanzania, by Mengwa, *Stuhlmann 8611* (B, destroyed).]

Aneilema tacazzeanum sensu Chiovenda, Missione Biol. Paese Borana, 4:305, 1939 [pro *Cufodontis 705*, non Hochstetter ex A. Richard (1850)].

Perennial or annual herbs (habit types IA, IB, IC, IIA4, and IIIA, Figures 1, 2). Roots fibrous. Shoots erect or ascending to decumbent, sparsely to densely branched, sometimes thickened at the base, 20–60(–100) cm tall. Internodes (0.7–)2–15.5 (–19.5) cm long, puberulous at least below the nodes (rarely completely glabrous). Leaves spirally arranged (rarely distichous), sheaths 0.5–2.5 cm long, puberulous or pilose-puberulous, ciliate at the apex, laminae petiolate (the upper several on the flowering shoot sessile), often gradually reduced towards the terminal inflorescence, narrowly lanceolate or lanceolate-elliptic to lanceolate-ovate, ovate-elliptic or ovate, (2.5–)3.5–11(–13.5) cm long, (0.6–)1–3.5(–4.5) cm wide, apex acute to acuminate (rarely obtuse), base cuneate to rounded, in the upper leaves sometimes subcordate- or cordate-amplexicaul, margin often undulate, scabrid and ciliate, both surfaces usually lustrous (sometimes the adaxial dull), adaxial usually pilose-puberulous (occasionally puberulous), abaxial puberulous or pilose-puberulous, the uniseriate hairs, when present, typically shorter than those on the adaxial surface; veins sometimes pale on the adaxial surface.

Inflorescences thyrses (Plate 2*m,o*), terminal on the main flowering shoots and frequently on axillary inflorescence-shoots from the inflorescence bract and upper leaves (also frequently terminal on longer, perforating or non-perforating, axillary shoots), moderately lax, ovoid, to 7(–9.5) cm long and 6.5(–9.5) cm wide, with 1–16(–19) cincinni, alternate (or a few sub-opposite), patent to ascending. Peduncles (1.7–)3–18.5(–21.5) cm long, puberulous. Inflorescence bract supramedial to medial, usually herbaceous, foliaceous or bract-like (Plate 2*o*). Inflorescence axis puberulous. Cincinni to 4(–7) cm long and 16(–33)-flowered. Cincinnus bracts membranous, appressed to the cincinnus peduncles or patent, occasionally reflexed, lanceolate or lanceolate-elliptic to ovate-elliptic or ovate, (1.7–)2–4.5(–5.5) mm long, not evidently glandular or with subapical glands apparent only in the youngest inflorescences, glabrous to puberulous. Cincinnus peduncles relatively uniform within the inflorescence or decreasing in the upper cincinni, exceeding the cincinnus bracts, (3.3–)4–10.5(–14) mm long, puberulous. Cincinnus axes puberulous. Bracteoles attached 1–4(–5) mm apart, membranous, ovate to ovate-lanceolate, sometimes slightly perfoliate at the base, (1.1–)1.3–2.6 mm long, to 0.5(–0.7) mm high, sometimes distinctly glandular near the apex, sometimes apparently eglandular, puberulous (rarely subglabrous), also with 1–several long uniseriate hairs towards the base or on the margin.

Flowers perfect and staminate, odorless, (6.5–)11–19 mm wide (Plate 2*m–p*). Pedicels (2.2–)2.5–5(–5.8) mm long in flower, to 7 mm long in fruit, horizontal to erect in flower, ± uniformly recurved in fruit 90°–220° (usually ~180°) (Figure 35*a*), persistent, puberulous at least apically. Sepals glandular near the apex with unlobed glands, puberulous and frequently with a few uniseriate hairs; medial sepal lanceolate or lanceolate-elliptic to ovate or ovate-elliptic, 2–5.2 mm long, (1.7–)2–3 mm wide, subapical gland prominent; lateral sepals ovate-elliptic to ovate or ovate-orbicular, 2.2–5.1 mm long, (2–)2.2–3 mm wide, subapical gland not prominent. Paired petals 4.5–9.5 mm long, (3.5–)4.5–11 mm wide, limb broadly ovate to ovate-deltate (occasionally ovate, rarely ovate-reniform), 3–6.5 mm long, white to lilac or pinkish purple (RHS colors: 76A-B, *Faden et al. 74/326;* 76B-C, *Andrews s.n.* cultivated; 76C, *Faden & Faden 74/291,* cultivated; 87D, *Faden & Faden 74/1183*), apex rounded to truncate (rarely slightly emarginate), margin crenulate to subentire; claw (1–)1.5–3(–4) mm long, concolorous with limb or paler basally, glabrous. Medial petal cup-shaped, ovate to obovate, broadest at the margin (viewed from the apex), which is slightly revolute, not retaining the lateral stamens when the flower opens, 3.5–7.5 mm long, 3–8 mm wide, 1.5–3.7 mm deep, concolorous with the limbs of the paired petals (Figure 23*a–c*). Lateral stamen filaments fused basally to medial stamen filament and occasionally to lateral staminode filaments (Figure 26*b*), medial staminode free. Medial staminode filament (1.2–)1.5–3.5 mm long, white to lilac basally, shading to yellow above (occasionally entirely yellow), antherode bilobed, yellow, lobes sessile or subsessile, obovate-cuneate, orbicular, transversely elliptic or broadly ovate, (0.25–)0.3–1.1 mm long, connective not or scarcely elongate. Lateral staminodes with filaments 2–4.5(–5.2) mm long, white to lilac below the middle, shading to yellow above, antherodes yellow, bilobed, similar in size and form to that of the medial staminode. Lateral stamens with filaments parallel (occasionally slightly divergent) near the base, then convergent and crossing about the middle to near the apex (rarely not crossing) (Figure 26*b;* Plate 2*n,p*), (3.8–)4.5–10 mm long, S-shaped, decurved after ~basal $^1/_3$ of their length, anthers ovate to ovate-elliptic (rarely lanceolate-elliptic to elliptic), 0.55–1.3 mm long, 0.45–1.1 mm wide, pollen yellow (rarely whitish). Medial stamen with filament 3–7 mm long, anther ovate-elliptic to ovate or ovate-lanceolate, saddle-shaped, 0.9–2.7 mm long, 0.6–1.3 mm wide, pollen yellow (occasionally orange-yellow), usually concolorous with the pollen of the lateral anthers. Ovary stipitate, obovate to obovate-subquadrate, 1.25–2.1 mm long, 1–1.5 mm wide, densely and uniformly covered with patent, glandular hairs, apex truncate, dorsal locule very prominent, 1-ovulate, ventral locules each 2-ovulate; style 2.5–9.8 mm long, decurved after the ovary and straight or gently arcuate-decurved for most of its length, also generally strongly curved out of the floral midplane (Plate 2*n,p*), stigma capitate, held at the same level as the lateral

anthers and in front of them, lateral to them or in contact with one of them.

Capsules (Figure 35*a,b*) stipitate, obovate to subquadrate (occasionally obovate-oblong), dehiscent, bivalved, trilocular, (3.4–)4.5–7.5(–9) mm long, (2.4–)3.3–5(–5.5) mm wide, carinate middorsally, pale gray or brown, peppered with numerous, small, dark brown and/or black spots, lustrous, puberulous, apex emarginate (occasionally truncate), dorsal valve deciduous, dorsal locule very prominent, humpbacked, 1-seeded or, by abortion, empty, ventral locules each 2-(or, by abortion, 1-)seeded, cells of the capsule wall transversely elongate or irregular. Dorsal locule seed (Plate 6*a*) ± hemispherical, humpbacked towards the capsule apex, 2.3–3.4 mm long, 2–2.6 (–3.1) mm wide, 1.6–2.1 mm thick, hilum dark brown, in a shallow groove, ± equal to the seed length, testa orange-buff (occasionally orange-brown or flesh pink), smooth, lacking farinose granules. Ventral locule seeds (Plate 6*a*) ovate to oblong or rectangular, apical seeds acute to obtuse or rounded apically, basal seeds rounded to truncate basally, (1.3–)1.5–2.6(–2.9) mm long, 1.6–2.3(–2.6) mm wide, 1–1.8 mm thick, hilum dark brown, usually not in a groove (occasionally in a very shallow groove), slightly extended onto apical or basal surface, testa orange-buff (occasionally buff), shallowly scrobiculate, not farinose or sparsely blackish farinose in the depressions and sometimes around the hilum and embryotega.

Key to the Subspecies of *Aneilema petersii*

Perennials; short, perforating, inflorescence-bearing shoots absent from the lower nodes of the main shoots; flowers 15–19 mm wide; sepals (3.3–)3.5–5.2 mm long; paired petals lilac to pinkish purple, 7–9.5 mm long, with claws 2–3(–4) mm long; styles (6.5–)7.5–9.8 mm long . . . . . *A. p.* subsp. ***petersii***

Annuals; short, perforating, inflorescence-bearing shoots usually produced from the middle and lower nodes of the main shoots; flowers (6.5–)11–15 mm wide; sepals 2–3.4(–3.8) mm long; paired petals white to very pale lilac, 4.5–7(–7.8) mm long, with claws (1–)1.5–2 mm long; styles 2.5–6.5 mm long . . . . . *A. p.* subsp. ***pallidiflorum,*** new subspecies

1a. *Aneilema petersii* (Hasskarl) C.B. Clarke subsp. *petersii*

HABITAT.—Grassland with scattered shrubs, bushland, thicket margins, wooded grassland, woodland, lowland forest margins, roadsides, cultivation, occasionally in damp situations, rarely in rocky places; sandy soil; full sun to dense shade; 0–500(–1100) m.

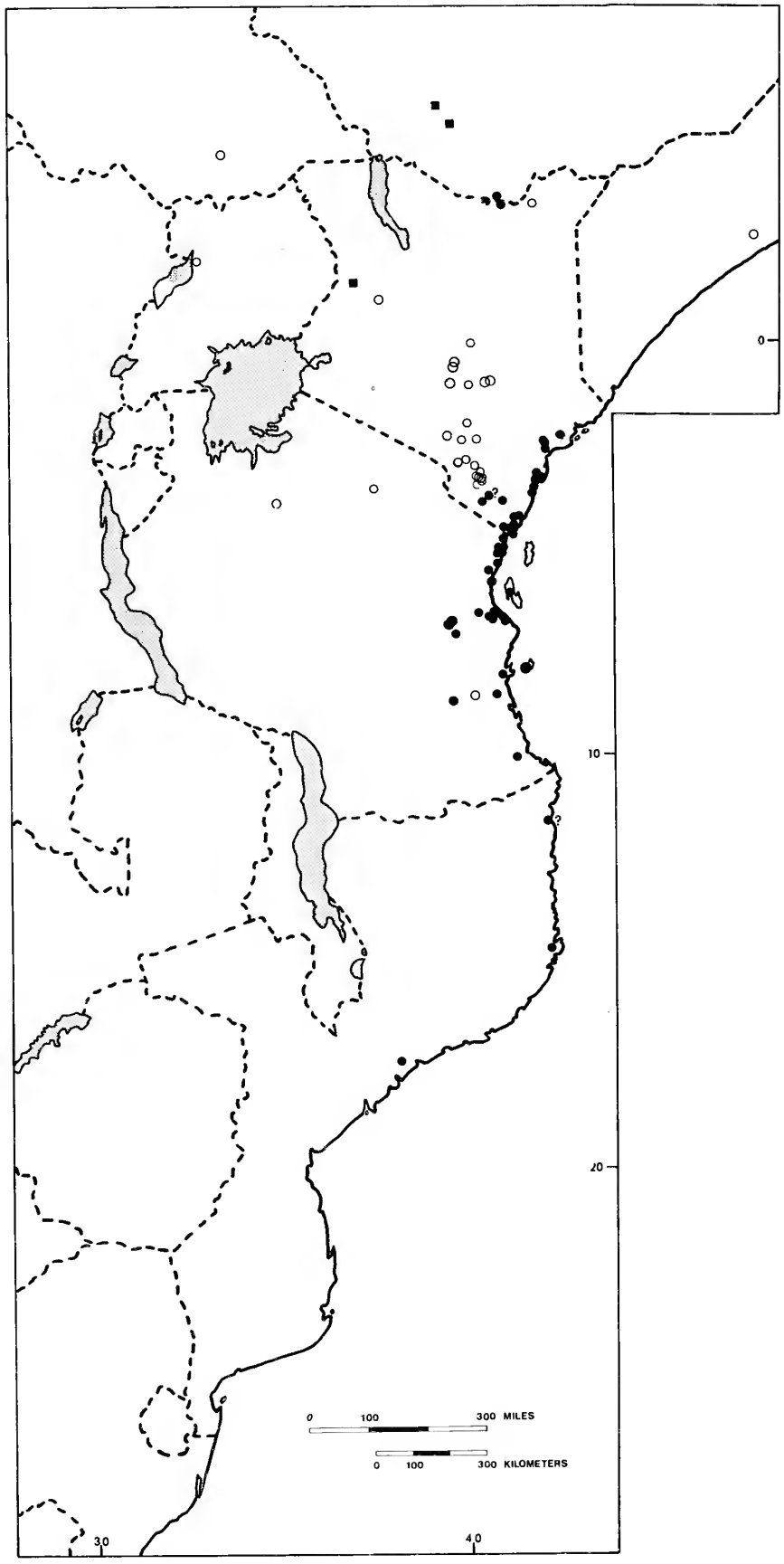
FLOWERING.—Flowering specimens have been seen from all months except December. In the field the flowers of one population opened from 0600–0630 hrs and faded between 1100–1130 hrs (Figure 25). Two other populations were noted as fading about 1030 hrs.

CHROMOSOME NUMBER.—$n = 13$, $2n = 26$.

DISTRIBUTION.—S Ethiopia to N Kenya and coastal and subcoastal Kenya to Mozambique (Map 10).

SPECIMENS SEEN.—ETHIOPIA. SIDAMO: ~10 km verso Mega [from] Moyale, *Cufodontis 705* (FT).

KENYA. District unknown: 5 mi W [of] Kisuvi jet, *Moomaw 951* (EA); Kenya Coast, *Rawlins 239* (EA). KILIFI: Sokoke Forest, ~3 km on track S of Gede to Jilore Forest Station, ~3°18′S, 39°57′E, *Faden & Faden 74/1237* (MO); 2.5 km Kakoneni–Jilore Forest Station road, 3°11′S, 39°52.5′E, *Faden et al. 72/38* (EA, K); Arabuko, *Graham 1848* [= *K1848*] (EA—2 sheets, K, MO); Sokoke Forest, *Jeffery K80* (EA, G (data different on this sheet), K); Sokoke Forest, *Saunders in EA11211* (EA); Kakoneni, ~20 km W of Malindi, *Spjut 3812* (EA); Mida, *Tweedie 3183* (K). KILIFI/LAMU: N of Mombassa [sic] to Lamu and Witu, 1902, *Whyte s.n.* (BM). KWALE: Near Kivukoni [Kivumoni] entrance to Shimba Hills National Reserve, *Bally & Smith B14357* (EA, K); Shimba Hills National Reserve, Campsite No. 1, *Faden & Evans 70/819,* cultivated Missouri Botanical Garden (EA, MO); Buda Forest, 4°27′S, 39°23′E, *Faden & Faden 74/291* (EA, MO); ~7 km past crossing of Ramisi River on Ramisi–Mrima Hill road, ~4°32′S, 39°19′E, *Faden & Faden 74/308* (M0); Kwale, *Graham 1903* [= *K1903 & Q522*] (EA—3 sheets, K—2 sheets, MO); between Umba and Mwena Rivers, *Lucas et al. 256* (EA, K); Shimba Hills, Tanga road near Marere Water Works, *Magogo & Glover 906* (EA, K); Kwale, *McKeag* [or *McCraig*] in *CM9187* (EA—2 sheets); S of Mombassa [sic] to Shimoni, 1902, *Whyte s.n.* (BM); Shimoni, S of Mombasa, 1902, *Whyte s.n.* (K). LAMU: Mambosasa Game Forest Post along Ziwa la Mkuni, 2°23′S, 40°32′E, *Faden & Faden 74/1142* (BR, EA, FT, K, MO, PRE, US); Witu, *Rawlins in EA11280* (EA, K). NORTHERN FRONTIER: Mt. Burrole just SW of Sololo, *Bally & Smith B14873* (EA, K); Moyale, 3°32′N, 39°03′E, *Gillett 14091* (B, BR, EA, K). TANA RIVER: 105 km N of Malindi on Garsen road, cultivated Missouri Botanical Garden, *Andrews s.n.* (EA, K, MO); Garsen–Malindi road, 1.5 km towards Malindi from turnoff to Oda, *Faden & Faden 74/1183* (EA, G, K, LISC, MO, PRE, US); Garsen–Malindi road, ~8 km from Garsen, ~2°22′S, 40°07′E, *Faden et al. 72/228* (C, EA, K, MO, US). TEITA: 10



MAP 10.—Distribution of *Aneilema petersii* (Hasskarl) C.B. Clarke subsp. *petersii* (solid circles), *A. petersii* subsp. *pallidiflorum* Faden, new subspecies (open circles), and *A. sebitense* Faden, new species (solid squares).

km Taru-Mackinnon Road on Nairobi-Mombasa road, 3°44′S, 39°04′E, *Faden & Faden 72/88* (EA, K, US, WAG); Mt. Kasigau, *Faden et al. 69/453* (EA, K); Taru Desert near Maungu, *Tweedie 3365* (K).

TANZANIA. BAGAMOYO: Bana Forest Reserve, *Mgaza 781* (EA, K); Kerege, Dar es Salaam, Sector 30 of Tsetse Research Unit, *D.C. Robertson in TRU518* (EA, K); Chambezi Agricultural Station, 6°35′S, 38°55′E, *S.A. Robertson 529* (EA, K); 2 mi E of Ruvu River, *Tweedie 1624* (K). KILWA: Selous [Game Reserve], Madaba, 8°35′S, 37°45′E, *Vollesen 3350* (EA). LINDI: 40 km W [of] Lindi, Lutambasee, *Schlieben 5942* (B, BM, BR, G—2 sheets, M, S). MOROGORO: 3 mi N [of] Tununguo, 30 mi SE [of] Morogoro, *Boaler 626* (BR, EA, K, NY, PRE); Boma, Morogoro Town, *Harris BJH5266* (MO); No. 1 Fly Round, 10 mi NE of Kingolwira Station, Morogoro, *Welch 243* (EA, K—2 sheets). PANGANI: Bushiri, *Faulkner in K712* (K—2 sheets); Mkwaja Ranch, ~5°40′-5°47′S, *Kloetzli et al. 144* (EA); Mwera-Mganbo [Mgambo] road, *Richards 21988* (K). RUFIJI: Mohoro, *Braun 3624* (EA); Mafia Island, Kilindoni, *Greenway 5236* (EA, K, PRE); Mafia Island, *Wallace 810* (K). RUFIJI/KILWA: Without locality, *Busse 3054* (EA). TANGA: Tanga, *Archbold 1491* (EA, MO); Totohovu [Mtotohovu] bf. Moa, *Braun 1377* (EA—2 sheets); without locality, *Busse 2281* (EA); 5 mi SE of Ngomeni, *Drummond & Hemsley 3610* (B, BR, EA, K—2 sheets, S); 9 km Tanga-Gombero road from Tanga-Mombasa road junction, ~5°00′S, 38°58′E, *Faden et al. 74/326* (B, BR, C, COI, DSM, EA, FT, K, LISC, MO, P, PRE, S, US, WAG); Kange Estate, *Faulkner 838* (BR, K—2 sheets, S); Pongwe-Maweni, *Faulkner 3670* (K, MO, SRGH) & *Faulkner s.n.* (EA, K); Amboni b. Tanga, *Geilinger 133* (K, Z) & *155* (K, Z) & *642* (Z); Tanga, *Volkens 175* (BM, G, K). UZARAMO: 5 mi up Bagamoyo road [from Dar es Salaam], *Batty 162* (K); Morogoro-Dar es Salaam road, Bamba, 6°44′S, 38°51′E, *Faden et al. 70/686A* (EA, K); near Dar es Salaam airport, *Harris 1484* (EA) & *BJH3069* (EA, MO); 3 mi NE [of] Dar es Salaam on Bagamoyo road, *Harris 2045* (EA); Dar es Salaam, Ubungo-Kigogo road, *Harris BJH2848* (EA); Dar es Salaam, *Harris BJH3413* (EA); Kunduchi, 16 km NNW of Dar es Salaam, 6°41′-43′S, 39°13′-14′E, *Harris & Tadros BJH5721* (EA); ~9.5 km E of R. Ruhu [Ruvu], *Milne-Redhead & Taylor 7437* (BR, EA, K—2 sheets, LISC). ZANZIBAR: Without locality, 1847-1852, *Boivin s.n.* (P); Bord de la mer, *Sacleux 1142* (P; photo K); Bet-el-ras, *Vaughan 2106* (BM).

MOZAMBIQUE. Without locality, Festland, an feuchten Orten, undated, *Peters s.n.* (B). NIASSA: Mouth of Msalu River, *Allen 94* (K); Mussovil [Mossuril] & Cabeccira, 1884-1885, *Carvalho s.n.* (COI). ZAMBEZIA: ~9 km de Nicuadala [on] estrada para Namacurra, *Torre & Correia 14296* (LISC).

1b. *Aneilema petersii* (Hasskarl) C.B. Clarke subsp. *pallidiflorum* Faden, new subspecies

Ab subsp. *petersii* habitu annuo, floribus parvioribus ((6.5-)11-15 mm latis), sepalis parvioribus (2-3.4(-3.8) mm longis); petalis lateralibus albis vel perpallide lilacinis et parvioribus (4.5-7(-7.8) mm longis) unguibus (1-)1.5-2 mm longis, stylo parviore (2.5-6.5 mm longo) differt.

TYPE.—Kenya, Teita [Taita on label] District, Irima Rock above Irima Water Hole, 3°18′S, 38°33′E, 24 Apr 1974, *Faden & Faden 74/237* (US, holotype; BR, EA, K, MO, PRE, WAG, isotypes).

HABITAT.—Deciduous bushland and bushland thickets commonly dominated by species of *Commiphora* and *Acacia*, frequently on rocky hills and outcrops, also recorded from grassland, woodland, riverine thickets, roadsides, and in swampy situations; sandy soil; partial shade to full sun; (125-)500-1000 m.

FLOWERING.—Flowering specimens have been seen from February to June and August (Kenya and Tanzania), September (Sudan and Uganda), and November (Somali Republic). Flowers of populations in the Tsavo area of Kenya open from 0545 to 0630 hrs and fade 1030-1100 hrs.

CHROMOSOME NUMBER.—$n = 13$, $2n = 26$.

DISTRIBUTION.—S Sudan to N Kenya and S Somali Republic S to Uganda and N and SE Tanzania (Map 10).

SPECIMENS SEEN.—SUDAN. EAST EQUATORIA: 10 km S of Mongalla, by Juba Road, *Lock 81/275* (K), cultivated Smithsonian Institution (US).

SOMALI REPUBLIC. BALAD: Hilweyne area along Balad-Mogadishu road, *Thulin & Warfa 5280* (UPS).

UGANDA. BUNYORO: 23 mi N of Butiaba turnoff on Butiaba-Murchison Falls National Park road, *Faden et al. 69/1068* (BR, EA).

KENYA. BARINGO: Chemolingot borehole area, Acheptopokwa River, ~0°58′N, 35°57′E, *Timberlake 344* (EA); approximately same locality, *Timberlake 156a* (EA). EMBU: Thuchi R. crossing on Embu-Meru road, 0°25′S, 37°52′E, *Gillett & Mathew 19068* (EA, K) & *19073* (EA); by Tana R., ~0°28′S, 37°55′E, *Gillett & Mathew 19090* (BR, EA, K). FORT HALL: 31 mi Embu-Kangonde, ~1 mi S of suspension bridge, 0°50′S, 37°40′E, *Faden et al. 69/395* (EA, K, MO, US). KITUI: Thika-Garissa road, 6 km Nguni-Enziu, 0°50′S, 38°17′E, *Faden & Faden 74/751* (BR, EA, FT, K, MO, PRE, US, WAG); Thika-Garissa road, 6.2 km Ukazzi-Garissa, 0°48′S, 38°35′E, *Faden & Faden 74/753* (B, BM, C, DSM, EA, G, K, M, MO, P, UPS, US); Mutomo Hill Plant Sanctuary, 1°51′S, 38°13′E, *Gillett 18604* (EA, K); Nairobi-Garissa road, ~5 km E of Ukazzi, ~0°48′S, 38°37′E, *Gillett & Gachathi 20488* (BR, EA, K, MO, PRE); Tsavo National Park E, Ithumba, *Hucks 221* (EA, K, Tsavo Research Centre); Mutomo Hill, *Mathew & Hanid 6061* (EA, K). KITUI/TANA RIVER: Katumba Hill, 92 km on the Garissa-Nairobi road, ~0°44′S, 38°48′E, *Gilbert & Thulin 1730* (EA, F). MACHAKOS: Near Hunter's Lodge, first rocky hill with baobabs on Nairobi-Mombasa road, 2°13′S, 37°43′E, *Faden & Faden 77/310* (EA, F, K, US); Tsavo National Park W, Chyulu Hills foothills, ~2°45′S, 37°58′E, *Faden et al. 69/617* (BR, EA, K, MO); Tsavo National Park W, 3 km WNW of Kyulu Station, 2°56′S, 38°23′E, *Gillett 17271* (BR, EA, K); "Bushwackers Safari Camp" (Masaleni), 2°19′S,

38°07′E, *Napper & Kanuri 2087* (EA, K, LISC, WAG); Tsavo National Park, S of Mtito Andei, *Strid 2406* (EA); first baobab rock outcrop few km beyond Simba, *Verdcourt 5234* (MO). MERU: Meru National Park, S of Point 40, new road crossing Kiolu River, *Ament & Magogo 263* (EA). NORTHERN FRONTIER: Dandu, 3°26′N, 39°54′E, *Gillett 13132* (B, BR, EA, K—2 sheets, PRE, S). TEITA: Tsavo National Park E, Irima Rock above Irima Water Hole, *Faden & Faden 72/284* (B, EA, FT, K, MO) & *74/237* (BR, EA, K, MO, PRE, US, WAG) & *77/342* (EA, F, US); Tsavo National Park E, Simba Hill, 3°22′S, 38°35′E, *Faden & Faden 74/231* (MO) & *74/231A* (BR, EA, K, MO, PRE, US, Z); 1.5 km from Nairobi–Mombasa road on E turnoff to Voi, 3°24′S, 38°35′E, *Faden & Faden 74/246* (BR, C, EA, K, MO, US); 2.8 km on Voi–Taveta road from Nairobi–Mombasa road junction, 3°25′S, 38°32′E, *Faden & Faden 74/274* (EA, MO); 7.3 km on Voi–Taveta road from Nairobi–Mombasa road junction, 3°26′S, 38°30′E, *Faden & Faden 74/529* (EA, K, MO, PRE, US); Tsavo National Park E, Voi Gate, *Gillett 17204* (BR, EA, K); Tsavo National Park E, Mudanda Rock, *Hucks & Hucks 15* (EA); Tsavo National Park E, Irima, 3°17′S, 38°32′E, *Hucks 669* (Tsavo Research Centre) (mixture with *A. rendlei*); Tsavo National Park E, Worsessa, ~3°20′S, 38°33′E, *Hucks 690* (EA, Tsavo Research Centre); Tsavo East National Park, Voi Gate camp site, *Msafiri 256* (EA); Ndi Mountain, opposite Manga Mountain, *Verdcourt & Polhill 2708* (BR, EA, K, PRE).

TANZANIA. KILWA: Selous Game Reserve, Kingupira, 8°28′S, 38°33′E, *Vollesen 1964* (EA). MBULU: Lake Manyara National Park, Bagayo River, *Greenway & Kanuri 11871* (BR, EA, K, PRE). SHINYANGA: Shinyanga, *Bax 368* (BR, K).

DISCUSSION

The unambiguous typification of *Aneilema petersii* is possible only because of the fortuitous survival of the type in the Berlin Herbarium. Despite its detail, the description of *Lamprodithyros petersii* by Hasskarl (1864a) would in itself have been inadequate to distinguish *A. petersii* from the closely related *A. indehiscens*, which also occurs in Mozambique.

The smaller packet on the Peters' type contains a capsule of *A. schlechteri*. The rarity of that species—it is known from only four collections (see Faden, 1984)—suggests that the capsule probably came from the type (*Schlechter 11748*), because that is the only collection of *A. schlechteri* known to have been in the Berlin Herbarium. Schlechter's collection was made in 1897 and, therefore, it could not have been the basis for any part of Hasskarl's description of *Lamprodithyros petersii*.

Both *Aneilema tetraspermum* K. Schumann and *A. sacleuxii* Hua are clearly synonyms of *A. petersii* subsp. *petersii*. The three specimens seen of *Volkens 175*, isosyntypes of *A. tetraspermum*, all have *"Aneilema leptasperma* K. Schum." on the label, a name Schumann never published. Clarke has written on the Kew sheet that "K. Schumann...altered his new specific name before publication, but forgot to alter his old specific name on the set distributed to Kew." Because all the original material of *A. tetraspermum* in the Berlin Herbarium was destroyed, the Kew sheet of *Volkens 175* is here selected as the lectotype.

Hua (1895) did not cite any specimen when he described *A. sacleuxii*. It is clear that *Sacleux 1142*—the "4" can easily be misread as a "9"—is the specimen on which the name was based because it matches Hua's description and apparently is the only collection of this species made by Sacleux.

Aneilema chrysanthum K. Schumann, the type of which did not survive in Berlin, is probably a synonym of *A. petersii* subsp. *petersii*. The type locality and certain characters in Schumann's description of *A. chrysanthum* agree with *A. petersii*, especially the narrow leaves, lax "panicle" with well-spaced branches, short pedicels, stipitate, subplano-convex, lustrous, mother-of-pearl colored, strongly humpbacked, obtuse capsules, and relatively large seeds. Among the characters that disagree, the single staminode reported is not found in any *Aneilema*, so this was probably inaccurately observed; the bilocular capsule is not consistent with the description of the capsule as humpbacked, which strongly suggests a trilocular capsule; and the yellow petal color may just have been erroneous. The only yellow-flowered species from the same general area, *A. nyasense*, occurs in forest, not in "sandy bush," as recorded for *A. chrysanthum*. It further differs from the description of *A. chrysanthum* in so many significant ways, that it is unlikely to have been the same species.

Tweedie 3365 and *Allen 94* have been included in this species with some doubt because both collections are of plants that have just begun to flower and lack capsules. The former has been included in this species because of the flower color, recorded by the collector as pale mauve, and the form of the antherodes, as determined from a dissected bud. *Allen 94* agrees with *A. petersii* in more attributes than it does with *A. indehiscens*, the only other possibility, and it was collected within the known range of the former but not the latter. This specimen has therefore been treated as *A. petersii*.

The subspecific determinations of the four collections from the Kenya–Ethiopia border region are also somewhat doubtful. *Bally & Smith B14873*, *Cufodontis 705*, and *Gillett 14091* are morphologically similar to one another. Because preserved flowers of *Gillett 14091* from the Kew Herbarium are in the size range of subsp. *petersii* (sepals 3.9–4.9 mm long; lateral stamen filaments 9 mm long; style 7.7 mm long) but are too large for subsp. *pallidiflorum*, all three of these collections have been treated as subsp. *petersii*.

The most striking features of the fourth collection, *Gillett 13132*, that immediately separate it from the other three collections are its very large leaves (to ~13.5 × 4.5 cm) and capsules (to 9 × 5.5 mm), the maximum dimensions for both of these organs in *A. petersii*. While capsule size shows considerable variation within both subspecies, the leaf width of *Gillett 13132* is approached only by specimens of subsp. *pallidiflorum*. The Gillett collection also agrees with this subspecies in flowering sepal length (3–3.2 mm), as measured in preserved flowers from Kew. Only the lack of perforating

inflorescence-shoots would distinguish this collection from typical subsp. *pallidiflorum*, but perhaps this is merely a function of age, as has been noted in other collections of this subspecies, e.g., *Ament & Glover 263*. Overall, *Gillett 13132* much better conforms with subsp. *pallidiflorum* than with subsp. *petersii*.

The occurrence of both subspecies of *A. petersii* in the Kenya–Ethiopia border region at first seems unlikely in view of their apparently different precipitation requirements and nearly total geographic isolation in other areas. However, closer study reveals that *Gillett 13132*, treated as subsp. *pallidiflorum*, is geographically separate from the other three collections that were considered subsp. *petersii*, and that its locality, Dandu, is situated in a zone of lower mean annual rainfall (less than 255 mm) than Moyale (687 mm), where *Gillett 14091* was collected (*National Atlas of Kenya*, 1970). Thus the pattern of distribution for these populations of the two subspecies conforms with that found in other parts of their ranges, at least with regard to rainfall.

The two Mafia Island collections (*Greenway 5236; Wallace 810*) have unusually short bracteoles and narrow capsules. They are considered to represent a minor geographic variant unworthy of taxonomic recognition.

The recent collection from Somalia (*Thulin & Warfa 5280*) is unusual in its inflorescences composed of only two to three cinicnni; bracteoles all cup-shaped and perfoliate, with at most a single uniseriate hair; and capsule locules one-seeded. Further collections are needed in order to determine whether this is an atypical specimen, a local variant, or even possibly an undescribed species. If this is *A. petersii*, then it is closer to subsp. *pallidiflorum* because of its short, perforating inflorescence-shoots and short sepals and style.

The great variation in vegetative morphology in *A. petersii* is due to the occurrence of both annuals and perennials in the species. Subspecies *petersii* is always perennial. It typically has a definite base and produces ascending shoots. Occasionally it may also form longer, decumbent shoots that give rise to new plants. The main shoots are thickened at the base, at least during the dry season.

Subspecies *pallidiflorum* is consistently annual despite some collectors' notes (including the writer's on *Faden & Faden 72/284*) to the contrary. Although all plants in some populations are very reduced and clearly annual, some from other populations may have decumbent shoots with their habits impossible to determine by casual inspection. Repeated field observations indicate that even these decumbent plants live less than a year and flower only once before dying. Their phenology is discussed below.

Distichously arranged leaves have been noted in *A. petersii* only in two populations, both of subsp. *pallidiflorum* (*Faden et al. 69/617* and *Faden et al. 69/1068*). All the lateral shoots of the latter have this arrangement, at least in plants raised from seeds.

The leaves of subsp. *petersii* are typically narrower (to 3.2 cm wide) than those of subsp. *pallidiflorum* (to 4.5 cm wide). They are also proportionally narrower, never being ovate. Subcordate- to cordate-amplexicaul leaves are present only in subsp. *pallidiflorum*.

The presence of numerous, short, lateral, inflorescence-bearing shoots in subsp. *pallidiflorum* but not in subsp. *petersii* is concordant with the former's annual habit, which requires greater emphasis on seed production. This is accomplished in subsp. *pallidiflorum* partly through an increased number of inflorescences and flowers and partly through self-pollination. The short shoots usually emerge from the mouths of the sheaths of the upper leaves but perforate those of the lower leaves.

The inflorescence bract of the terminal inflorescence of the main shoot is generally longer in subsp. *pallidiflorum* than in the typical subspecies. In populations of the former in the Voi area of Kenya the inflorescence bracts are borne close to the inflorescences and are held erect. They thus form a dark green background for the white flowers, increasing the latter's visibility (Plate 2*o*).

The size ranges of floral parts are greater in *A. petersii* than in any other species of section *Lamprodithyros*. This is due in large measure to the reduced flower size in subsp. *pallidiflorum*, an attribute commonly associated with self-pollination in *Aneilema*. The last flowers produced in plants of this subspecies just prior to their death are particularly small. Flowers of the two subspecies differ consistently in size and petal color. The most reliable distinctions are included in the key.

Differences in the capsules and seeds between the two subspecies are largely qualitative. Their reliability is uncertain due to insufficient material from some critical areas such as Mozambique (subsp. *petersii*), northern Tanzania (subsp. *pallidiflorum*), and the Kenya–Ethiopia border region (both subspecies). On the basis of available material, the capsules of subsp. *pallidiflorum* are more obovate (versus subquadrate), more deeply emarginate apically and browner (versus grayer) than those of subsp. *petersii*. The ventral locule seeds of subsp. *pallidiflorum* are regularly blackish farinose, while those of subsp. *petersii* often completely lack farinose granules. The apical ventral seeds are usually more pointed in the former.

The difference in flowering phenology between the two subspecies is striking and is largely due to the rainfall distribution patterns in the regions in which they occur (Jackson, 1961; *National Atlas of Kenya*, 1970). Throughout the range of subsp. *petersii* there is no consistently dry month. Hence it may be expected in flower in every month in some part of its range. The lack of flowering specimens from December is almost certainly an artifact. *Faden et al. 72/38*, collected on 10 January, has mature fruits and must have been flowering in December.

For subsp. *pallidiflorum*, the flowering phenology is well understood only in eastern Kenya. There are two distinct rainy seasons, March to May and October to December. Observations in the Tsavo area indicate that the plants come up with the October to December rains but do not flower then. Many of them survive the following dry season and flower during the

March to May rains. All of them die during the subsequent dry season. In the Ugandan locality the rainy season spans the coincident dry months of the Kenyan and Tanzanian sites, so it is not surprising that the single collection from Uganda was flowering at a very different time of year from the other collections.

A single exception to this pattern has been recorded. In 1977, the rains in Kenya, which should have ended in December 1976, continued into January. Consequently, a few plants of subsp. *pallidiflorum* in Tsavo National Park were found in flower in February 1977 in what would normally have been the height of the dry season.

Five collections made since my original treatment of this species (Faden, 1975) have greatly extended the known range of subsp. *pallidiflorum:* to the Sudan (*Lock 81/275*), to the Somali Republic (*Thulin & Warfa 5280*), to western Kenya (*Timberlake 344* and *156a*), and to southern Tanzania (*Vollesen 1964*).

Aneilema petersii is a highly distinctive species. It can be separated from all other taxa of section *Lamprodithyros* by its mostly non-perfoliate bracteoles, some or all with long, uniseriate hairs basally, crossed lateral stamen filaments not retained by the medial petal, longly stipitate, dehiscent, broad capsules with a humpbacked, deciduous, dorsal valve, and strongly dimorphic seeds, the dorsal locule seed particularly large (largest seed in the section). Both subspecies have all of these attributes and are easily separated in the field using the key characters, many of which, unfortunately, do not preserve well in herbarium specimens.

Aneilema petersii appears to be most closely related to *A. indehiscens*, the only other species in section *Lamprodithyros* (except for *A. zebrinum*) known to lack a stamen retention mechanism. *Aneilema indehiscens* is also similar in its bracteoles sometimes not perfoliate and frequently with one or more uniseriate hairs on the margin, and in the antherodes of all three staminodes of similar form (to one another). For differences between these species, see the discussion of *A. indehiscens* and the key to the species.

2. *Aneilema indehiscens* Faden

Aneilema indehiscens Faden, Bothalia, 15:96, 1984.—Obermeyer and Faden in Leistner, Fl. Southern Africa, 4(2):40, fig. 9-2a,b, 1985. [Type: Kenya, Tana River District, Garsen–Malindi road, 1.5 km towards Malindi from turnoff to Oda, 2°32′S, 40°07′30″E, 22–24 July 1974, *Faden & Faden 74/1184* (US, holotype; BR, EA, FT, K, MO, PRE, WAG, isotypes).]

Aneilema petersii (Hasskarl) C.B. Clarke in De Candolle, Monogr. Phan., 3:225, 1881 [pro *Kirk* s.n.]; in Thiselton-Dyer, Fl. Trop. Africa, 8:70, 1901 [pro *Kirk* s.n.].

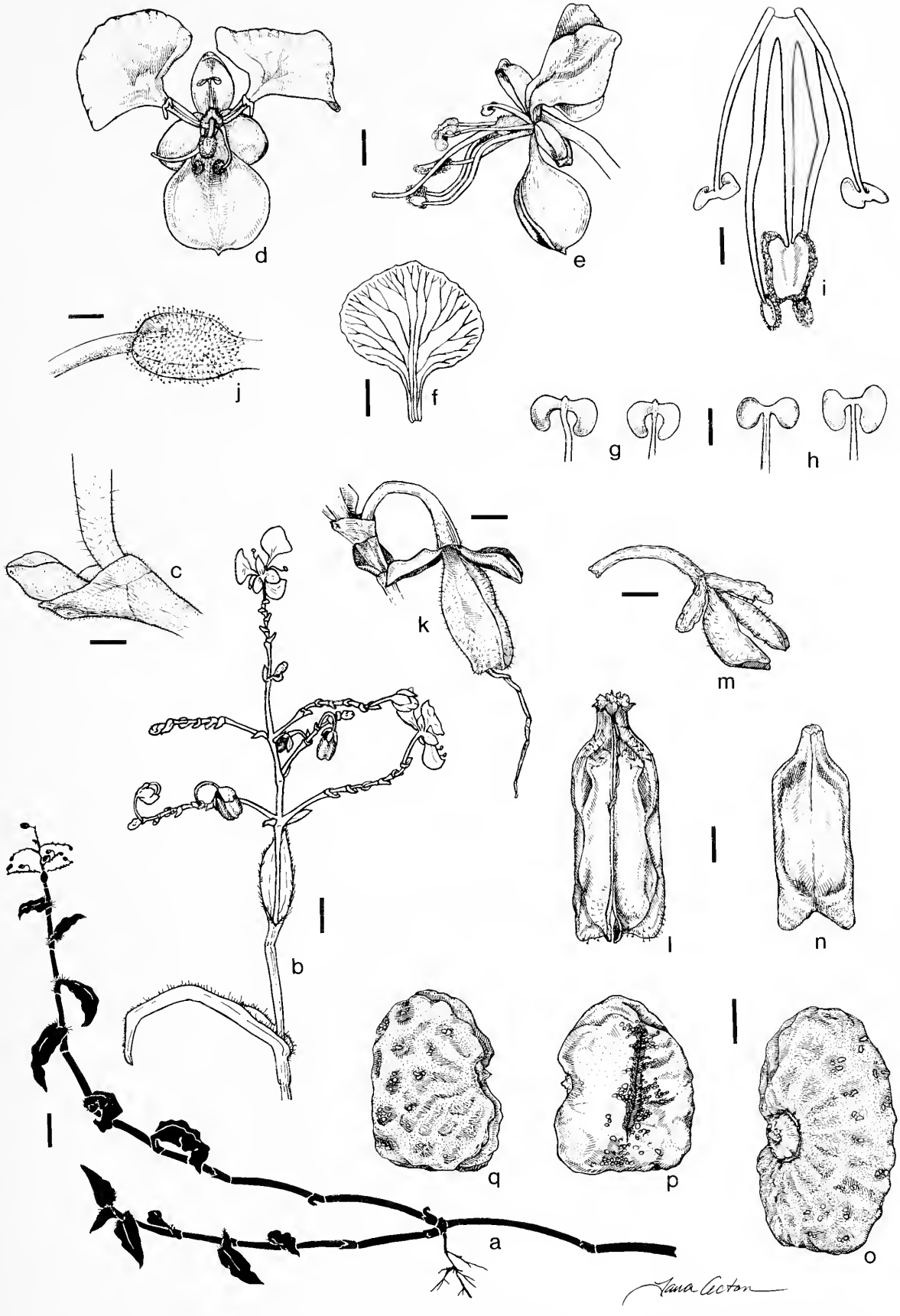
Aneilema dregeanum sensu Compton, Fl. Swaziland, 33, 1966, p.p. [non Kunth, 1843].

Perennial herbs (habit type IIA3, Figures 2, 48*a*). Roots fibrous. Vegetative shoots sparsely branched, trailing and often looping along the ground, occasionally rooting at the nodes, sometimes straggling through shrubs, to 3 m long (or longer?), flowering shoots produced irregularly, unbranched or sparsely branched, erect to ascending, to ~60 cm tall (reaching a greater height when straggling through shrubs). Internodes (1–)3–15 (–19) cm long, to 5 mm thick, glabrous or very sparsely puberulous and glabrescent. Leaves spirally arranged, sheaths 0.5–2 cm long, puberulous and sometimes sparsely pilose, ciliate at the apex, laminae shortly petiolate, gradually reduced towards the terminal inflorescence, narrowly lanceolate to lanceolate-elliptic, lanceolate-ovate, or ovate-elliptic, rarely ovate, (2.5–)3–10(–13) cm long, (0.7–)1–2.5(–3.5) cm wide, apex acuminate or acute, margin frequently undulate, scabrid, also ciliate at least basally and on the petiolate, both surfaces lustrous, puberulous, rarely densely pilose-puberulous, abaxial surface with with longer, more numerous, uniseriate, hairs, veins pale on the adaxial surface.

Inflorescences thyrses (Figure 48*b*), terminal and frequently axillary from the upper leaves on the flowering shoots, lax to moderately dense, ovoid to broadly ovoid, (2–)2.5–5(–8) cm long, (1.5–)2–5(–7) cm wide, with (1–)3–9 cincinni, ascending (the lower sometimes patent), mostly alternate (frequently some subopposite, rarely some subverticillate). Peduncles 2–5(–8) cm long, puberulous. Inflorescence bract supramedial to medial, herbaceous and foliaceous or membranous and bract-like. Inflorescence axis slightly zigzag, puberulous. Cincinni to 7.5 cm long and 27-flowered. Cincinnus bracts membranous, appressed to the cincinnus peduncles or patent, lanceolate-elliptic to linear-lanceolate or ovate, (1.5–)2–3(–5) mm long, glandular near the apex, glabrous to puberulous. Cincinnus peduncles relatively uniform within the inflorescence or decreasing in the upper cincinni, exceeding the cincinnus bracts, 3–11(–12.5) mm long, puberulous. Cincinnus axes puberulous. Bracteoles (Figure 48*c*) attached 1–3.5 (–4.5) mm apart, ± herbaceous, eccentrically cup-shaped, usually perfoliate, 1.3–2.6 mm long, to 1 mm high, with a prominent subapical gland, puberulous at least basally or medially, frequently also with 1-several, long, uniseriate hairs on or near the fused edge, margin sometimes slightly thickened (glandular?) near the fused edge.

Flowers perfect and staminate, odorless, (9–)13–17.5 mm

FIGURE 48.—*Aneilema indehiscens* Faden. *A. indehiscens* subsp. *indehiscens* (*a–g,i–l*): *a,* habit; *b,* inflorescence; *c,* bracteole; *d,* perfect flower, front view; *e,* perfect flower, side view; *f,* lateral petal; *g,* antherodes of staminodes: medial staminode (right) and lateral staminode (left); *i,* androecium, top view, medial staminode omitted, gynoecium removed; *j,* ovary and base of style, side view; *k,* capsule attached to cincinnus, side view; *l,* dorsal capsule valve, dorsal view (*a–c,* from *Faden & Faden 74/380; d–g,i–l,* from *Faden & Faden 72/72*); *A. indehiscens* subsp. *lilacinum* Faden (*h, m–q*): *h,* antherodes of staminodes: medial staminode (right) and lateral staminode (left); *m,* capsule, side view; *n,* dorsal capsule valve, dorsal view; *o,* dorsal locule seed, dorsal view; *p,* ventral locule seed, ventral view; *q,* ventral locule seed, dorsal view (*h,* from *Faden & Faden 74/208; m–q,* from *Faden & Faden 74/202*). (Bars = 40 mm for *a;* 10 mm for *b;* 2 mm for *d-f,k,m;* 1 mm for *c,g–i,l,n;* 0.67 mm for *j;* 0.5 mm for *o–q*.)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wide (Figure 48*d,e;* Plate 3*a,b*). Pedicels 3.8–6(–8) mm long in flower, to 10 mm long in fruit, erect or ascending in flower, ± uniformly recurved in fruit, usually ~180°, persistent, puberulous. Sepals glandular near the apex, puberulous; medial sepal ovate or ovate-elliptic to lanceolate-elliptic or lanceolate, 2.4–4.3(–4.9) mm long, 1.8–2.6 mm wide, subapical gland very prominent, ± distinctly bilobed; lateral sepals broadly elliptic or ovate-elliptic to ovate-orbicular, oblong-elliptic or obovate-elliptic, 2.6–4.3(–4.6) mm long, 2.2–3.2 mm wide, subapical gland prominent or not, usually unlobed (rarely bilobed). Paired petals 7.3–9.5 mm long, 6–8.5 mm wide (Figure 48*f*), limb broadly ovate to ovate-deltate, 4.3–6.5 mm long, white to very pale lilac (RHS colors: 76C, *Faden & Faden 74/202;* 84D, *Faden & Faden 74/208*), apex rounded or occasionally obtuse, claw 2–3.5 mm long, white or whitish, glabrous. Medial petal cup-shaped, obovate (occasionally ovate or suborbicular), broadest at the margin (viewed from the apex), 6–8 mm long, 4–6(–7.5) mm wide, 3–5 mm deep, concolorous with the limbs of the paired petals (Figure 23*d-f*). Stamen filaments shortly fused basally and also shortly fused with the lateral staminode filaments (Figures 26*a,* 48*i*). Medial staminode filament (1.5–)2.7–4.6 mm long, yellow above the white or whitish base, antherode (rarely absent) bilobed, yellow, lobes sessile to shortly stipitate, obovate-cuneate to sickle-shaped and decurved, 0.6–1.2 mm long, connective usually slightly elongate (Figure 48*g,* right, *h,* right). Lateral staminodes with filaments 4–5.6 mm long, white or whitish, shading to yellow at the apex, antherodes bilobed, yellow, generally similar in size and form to that of the medial staminode (Figure 48*g,* left, *h,* left). Lateral stamens with filaments usually ± parallel or slightly divergent for their entire length, or sometimes convergent apically (Figures 26*a,* 48*i;* Plate 3*a,b*), 7.7–8.5 mm long, gently S-shaped, geniculate below the middle, glabrous, anthers ovate to ovate-elliptic or occasionally elliptic to lanceolate-elliptic, 0.65–1.3 mm long, 0.6–1 mm wide, pollen yellow to orange or dirty white. Medial stamen with filament 5–7 mm long, anther ovate to ovate-elliptic, saddle-shaped, 1.5–2.4 mm long, 1.2–1.7 mm wide, pollen yellow to orange-yellow, concolorous with the pollen of the lateral anthers or different in color. Ovary substipitate (Figure 48*j*), obovate to oblong (rarely subquadrate), 1.5–2.3 mm long, 1.2–1.6 mm wide, densely and uniformly covered with patent, glandular hairs (very rarely mixed with a few hook-hairs), apex truncate to slightly emarginate, dorsal locule prominent, subequal to the ventral locules or distinctly smaller than them, 1-(or rarely 2-)ovulate, ventral locules each 2-(or very rarely 3-)ovulate; style 8–9.3 mm long, straight or gently arcuate-decurved for most of its length and strongly curved laterally out of the floral midplane (Plate 3*a,b*), stigma capitate, usually held in front of and lateral to the anthers.

Capsules (Figure 48*k–n*) subsessile to stipitate, obovate-elliptic to obovate-oblong, oblong or oblanceolate, dehiscent or indehiscent, when dehiscent, bivalved (occasionally partially trivalved), trilocular, (4–)4.5–6(–6.8) mm long, (1.9–)2.3–3 (–3.4) mm wide, chestnut brown or mottled dark and light brown or gray-brown, lustrous, puberulous, apex emarginate, valves persistent (very rarely dorsal valve deciduous), dorsal valve with dorsal locule truncate to rounded apically or sometimes terminating in a narrow ridge and subequal to the ventral valve (Figure 48*l*), dorsal locule prominent, 1-seeded or, by abortion, empty (very rarely 2-seeded), ventral locules each 2- or, by abortion, 1-seeded (very rarely 3-seeded); cells of the capsule wall transversely elongate. Seeds (Figure 48*o–q;* Plate 6*b*) elliptic, 2–2.9 mm long, 1.35–1.65(–1.9) mm wide (dorsal locule seed) or ovate to trapezoidal with apical seed obtuse to rounded apically and basal seed rounded to slightly angular basally, 1.5–2.2(–2.5) mm long, 1.3–1.8 mm wide (ventral locule seeds), 0.65–1 mm thick, hilum dark brown, in a very shallow groove or not in a groove, not extended onto apical and basal surfaces, testa usually orange-buff (rarely buff or orange-brown), very shallowly scrobiculate, with white farinose granules sparse to dense around the hilum, sparse around the embryotega and very sparse or lacking in the depressions.

Key to the Subspecies of *Aneilema indehiscens*

1. Petals white; capsule usually chestnut brown . . . . . ***A. i.*** subsp. ***indehiscens***
1. Petals pale lilac; capsules gray-brown or mottled light and dark brown.
   2. Capsules with dorsal locule rounded to truncate apically, not terminating in a ridge; pollen of medial and lateral anthers discolorous; Mozambique and Zimbabwe to South Africa . . . . . ***A. i.*** subsp. ***lilacinum***
   2. Capsules with ventral valve usually terminating in a ridge; pollen of all 3 anthers concolorous; western Kenya . . . . . ***A. i.*** subsp. ***keniense,*** new subspecies

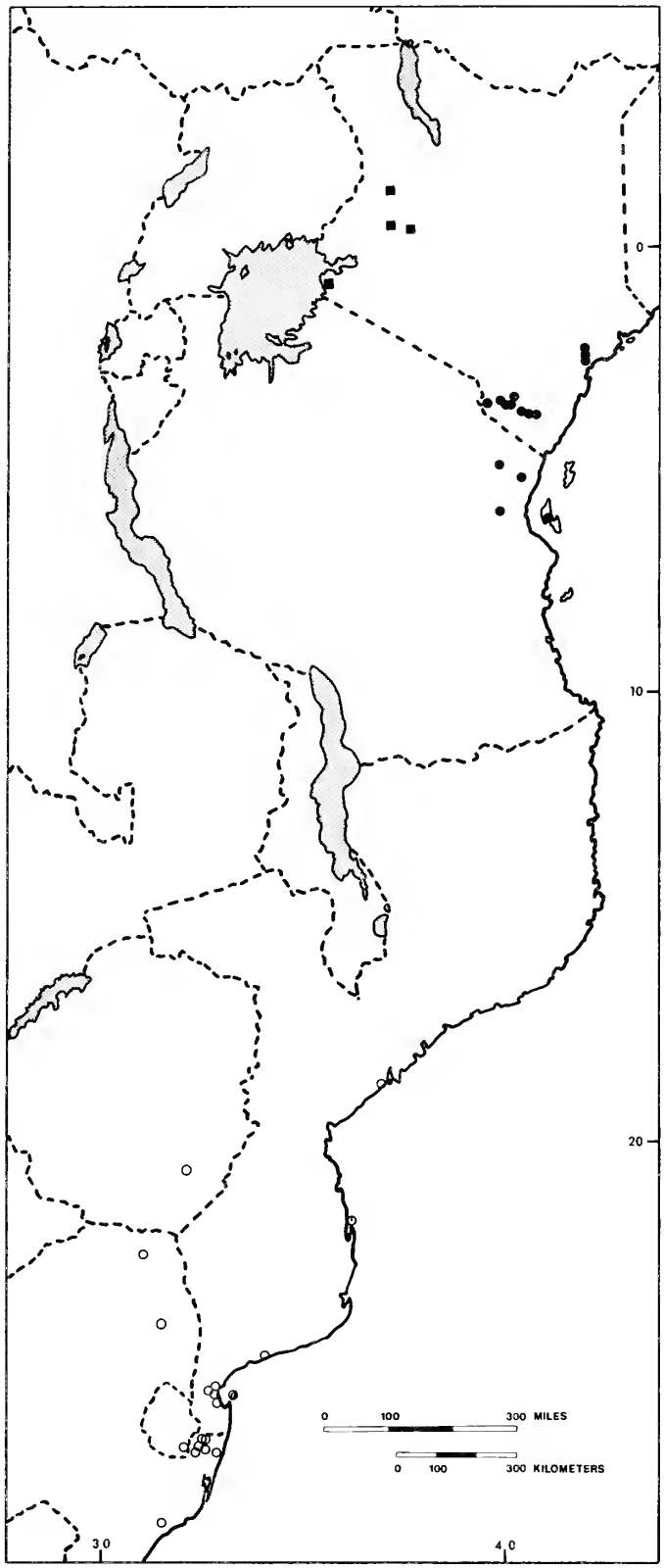
2a. *Aneilema indehiscens* Faden subsp. *indehiscens*

HABITAT.—Bushland and thickets of varied species composition; sandy or clayey soils; usually in partial shade; ~10–1050 m.

FLOWERING.—Flowering specimens have been seen from January, March–May, July and October. In the field the flowers open 0600–0630(–~0645) hrs and fade 1100–1230 hrs.

CHROMOSOME NUMBER.—$n = 26$, $2n = 52$.

DISTRIBUTION.—E Kenya and NE Tanzania (Map 11).



MAP 11.—Distribution of *Aneilema indehiscens* Faden subsp. *indehiscens* (solid circles), *A. indehiscens* subsp. *lilacinum* Faden (open circles), and *A. indehiscens* subsp. *keniense* Faden, new subspecies (solid squares).

SPECIMENS SEEN.—KENYA. TANA RIVER: Garsen, 2°16′S, 40°07′E, *Faden & Faden 74/1066* (B, EA, FT, K, MO, P, PRE, UPS, US, WAG); 0.8 km towards Garsen from turnoff to Kibusu on Malindi-Garsen road, 2°21′S, 40°07′E, *Faden & Faden 74/1173* (BR, C, EA, K, LISC, MO, US); Garsen-Malindi road, 1.5 km towards Malindi from turnoff to Oda, 2°32′S, 40°07′30″E, *Faden & Faden 74/1184* (BR, EA, FT, K, MO, PRE, US, WAG). TEITA: Voi-Taveta road, just E of Tsavo National Park East entrance gate, cult. University of Chicago, *A. Faden 3/79* (F, US); Tsavo National Park East, Buchuma (Bachuma) Gate, 3°40′S, 38°56′E, *Faden & Faden 72/72* (EA; cultivated Missouri Botanical Garden: BR, EA, K, MO, PRE, US); 28 km towards Taveta on Voi-Taveta road from turnoff on Nairobi-Mombasa road, 3°30′S, 38°19′E, *Faden & Faden 74/489* (BR, EA, K, MO, US); 18 km towards Taveta on Voi-Taveta road from turnoff on Nairobi-Mombasa road, ~3°30′S, 38°24′E, *Faden & Faden 74/532* (EA, MO); 26 km towards Taveta on Voi-Taveta road from Nairobi-Mombasa road turnoff, ~3°31′S, 38°21′E, *Faden & Faden 74/536* (EA, K, MO); 11.7 km towards Mombasa past Maungu Station on Nairobi-Mombasa road, 3°37′S, 38°50′E, *Faden & Faden 74/1284* (MO); mile post Taveta 36/Voi 36 on Taveta-Voi road, ~3°25′S, 38°10′E, *Faden et al. 69/318* (EA, FT, K, MO); Maungu Hills, 3°38′S, 38°44′E, *Faden et al. 70/158* (EA, K); 3 km E of Bura Railway Station, *Gillett 19562* (EA, K, MO); Voi, *Napier 973* (EA, K).

TANZANIA. BAGAMOYO: 4.5 km towards Mbwewe from crossing of Milgoji River on Korogwe-Dar es Salaam road, ~5°57′S, 38°12′E, *Faden & Faden 74/380* (MO; cultivated Missouri Botanical Garden: DSM, EA, K, MO); Mbwewe, *Faulkner 4471* (K). LUSHOTO: Mazinde, *Drummond & Hemsley 2337* (K). TANGA: Magunga Estate, *Faulkner 1160* (K). ZANZIBAR: Chumbuni, *Vaughan 1851* (EA, K).

2b. *Aneilema indehiscens* Faden subsp. *lilacinum*

Aneilema indehiscens Faden subsp. *lilacinum* Faden, Bothalia, 15:97, 1984.—Obermeyer and Faden in Leistner, Fl. Southern Africa, 4(2):40, fig. 9-2a,b, 1985. [Type: South Africa, Natal, Ingwavuma-Ndumu road, 15.5 km towards Ingwavuma from junction with Ndumu-Maputa road, ~27°06′S, 32°12′E, 16 Feb 1974, *Faden & Faden 74/202* (US, holotype; BR, EA, K, LISC, MO, NH, NU, PRE, WAG, isotypes).]

HABITAT.—Open forest, woodland, thickets, lowveld bush, and edges of marshes; sandy or clayey soils; usually in partial shade; ~10–550 m.

FLOWERING.—Flowering specimens have been seen from all months except August. In the field all flowers of one population were found fully open at 0700 hrs, while those of a second, nearby population began to fade at 1130 hrs. In cultivation the flowers of two populations were found to open about sunrise; they began to fade 4 and 6¼ hrs later, respectively.

CHROMOSOME NUMBER.—$2n = 52$.

DISTRIBUTION.—S Mozambique and S Zimbabwe to N Transvaal, Swaziland, and N Natal (Map 11).

SPECIMENS SEEN.—ZIMBABWE. District unknown: Bank of Lundi River, *Bayliss BS7216* (MO).

MOZAMBIQUE. LOURENÇO MARQUES: Costa do Sol, *Barbosa 655* (LISC); without precise locality, *Borle 364* (G); near Lourenço Marques town (Costa do Sol), *Gomes & Sousa 3441* (BR, K—2 sheets); Maputo, Sep 1930, *Gomes & Sousa s.n.* (LISC); Ricatla, Acajou wood, *Junod 493* (LISC, PRE–2 sheets); Inhaca Island, 23 mi E of Lourenço Marques, *Mogg 27469* (K); Inhaca, Picada Estacão Hotel, *Moura et al. 399* (US); Costa do Sol, *Pedro 109* (LMA); Matolla, *Quintas 64* (COI—2 sheets). MANICA E SOFALA: Mouth of River Melambe, Zambesi Delta, 8 Jul 1861, *Kirk s.n.* (K). SUL DO SAVE: Vila de Joãao Belo, Chipenhe, *Barbosa & Lemos 8431* (COI, K, LISC, LMA, PRE); Benguérua Isle, central ridge, *Mogg 28886* (SRGH).

SWAZILAND. HLATIKULU: Ingwavuma Poort, *Compton 28610* (K, PRE).

SOUTH AFRICA. TRANSVAAL: 2230 (Messina): 18 mi NE of Sibasa on road to Sambandou, *Codd 6891* (K, PRE). 2431 (Acornhoek): Manyeleti Game Reserve, Albatross koppie (-CB), *Bredenkamp 1795* (PRE). NATAL: 2632 (Bela Vista): Ndumu Game Reserve, near main Rest Camp, ~26°55′S, 32°19′E (-CD), *Faden & Faden 74/208* (K, MO, NH, NU, PRE, US); grid reference only (-CD), *Moll 4152* (EA, K, NH, NU, PRE); Ndumu Game Reserve, Ndumu Hill (-CD), *Oatley C6* (PRE); Ndumu Game Reserve, E of Polwe Pan (-CD), *Pooley 1399* (NU). 2732 (Ubombo): Jozini below dam, Makatini flats (-AC), *Brenan 14232* (K); Ingwavuma-Ndumu road, 15.5 km towards Ingwavuma from junction with Ndumu-Maputa road, ~27°06′S, 32°12′E (-A A), *Faden & Faden 74/202* (BR, EA, K, LISC, MO, NH, NU, PRE, US, WAG); Ubombo Flats (-AB), *Strey 10326* (EA, K, NH, NU, PRE); Lake Sibayi (-BC/D), *Vahrmeijer 693* (PRE); Mahatini Flats, *Vahrmeijer & Tölken 192* (PRE). 2831 (Nkandla): Eshowe, above reservoir (-CD), *Lawn 1289* (NH).

2c. *Aneilema indehiscens* subsp. *keniense* Faden, new subspecies

Ab subspecie *indehiscenti* petalis pallide lilacinis, capsulis griseo-brunneis vel pallide brunneis et atro-brunneis irregulariter maculatis differt; ab subspecie *lilacino* capsulis valva dorsali apice plerumque in crista terminanti, polline omnium trium antherarum concoloro differt.

TYPE.—Kenya, West Suk [West Pokot] District, Kerio Valley, Tot-Sigor road, 4.8 km before crossing of Weiwei River, ~1°26′N, 35°32′E, 14 Mar 1977; collected sterile, cultivated at the University of Chicago, pressed 17 Jul 1977, *Faden & Faden 77/788* (US, holotype; EA, F, K, isotypes).

HABITAT.—Thickets and thicket edges, ~1000–1250 m.

FLOWERING.—Flowering May and October to November.

CHROMOSOME NUMBER.—$2n = 52$.

DISTRIBUTION.—Western Kenya (Map 11).

SPECIMENS SEEN.—KENYA. BARINGO: Samatian Island,

Lake Baringo, *Birnie 9* (EA); same locality, *Lavranos 17063* (EA). ELGEYO: Tambach–Tot road, 10 km N of junction with Kabarnet–Tambach road, 0°37′N, 35°36′E, *Faden et al. 70/894A* (EA, K). SOUTH KAVIRONDO: Lambwe Valley, Riamkanga, 0°42′30″S, 34°12′E, *Faden 69/1300A* (EA). WEST SUK: Kerio Valley, Tot–Sigor road, 4.8 km before crossing of Weiwei River, 1°26′N, 35°32′E, *Faden & Faden 77/788* (EA, F, K, US).

DISCUSSION

Specimens of *Aneilema indehiscens* have usually been treated as other species. Clarke (1881a, 1901) considered *Kirk s.n.* (subsp. *lilacinum*) as *A. petersii*, and Compton (1976) cited *Compton 28610*, which is also subsp. *lilacinum*, as *A. dregeanum*. Ross (1972) did not cite any specimen referable to *A. indehiscens*, but he must have included the specimens he saw of this species, which is quite frequent in northern Natal, in *A. dregeanum* and/or other species.

The two collections of *A. indehiscens* from western Kenya that were part of mixed collections with *A. recurvatum*, *Faden 69/1300A* and *Faden et al. 70/894A*, were treated with some doubt as subsp. *indehiscens* in Faden (1975) but were omitted when that species was described (Faden, 1984). A third collection from the same region, *Faden & Faden 77/788*, has confirmed that these plants are consistently distinguishable from both described subspecies of *A. indehiscens*, and, consequently, subsp. *keniense* is described above. Subspecies *keniense* differs from subsp. *indehiscens* by its pale lilac flowers and paler, mottled capsules that are more distinctly stipitate. In these characters it agrees with subsp. *lilacinum*, from which it differs by its capsules with the dorsal valve usually terminating in a ridge, scarcity of uniseriate hairs on the bracteoles, relatively short pedicels (4.5–6.5 mm long), and concolorous pollen in all three anthers.

The long-trailing or straggling habit of *A. indehiscens* is quite characteristic and apparently constant. I have noted it in all 13 populations of subsp. *indehiscens*, both populations of subsp. *lilacinum*, and one population of subsp. *keniense* observed in the field. It is also maintained in cultivation. Plants persist during the dry season as thick, leafless shoots. A habit similar to that of *A. indehiscens* has been noted elsewhere in the genus only in *A. recurvatum* and in a single sterile plant believed to belong to *A. hockii*.

The inflorescences are often grouped into larger functional units. Such synflorescences (Troll, 1961) consist of a terminal thyrse, a secondary thyrse from the axil of the inflorescence bract, and frequently additional thyrses axillary to the uppermost foliage leaf (on the main shoot) and/or the inflorescence bract of the secondary inflorescence.

The bracteoles are usually perfoliate. Occasionally, however, one or more may be split to the base by the pedicels. *Faulkner 1160* and *Vaughan 1851* are unusual in having all of the bracteoles regularly non-perfoliate and thus similar to *A. petersii* in this character.

The number of uniseriate hairs on the bracteoles and the percentage of the bracteoles within an inflorescence to have such hairs show much variation. In general, uniseriate hairs are much more numerous and occur on more bracteoles in subsp. *lilacinum* than in the other subspecies.

The medial petal usually does not retain the lateral stamens when the flower opens. In one population (*Faden & Faden 74/489*, subsp. *indehiscens*), however, the stamens were held briefly but not in the usual manner. Only the filaments were contained in the petal; the anthers were shortly exserted. Furthermore, when the margins of the petal unfurled, the stamens rose slowly, indicating that they had not been under tension.

In one population of subsp. *indehiscens* (*Faden & Faden 74/1184*), the lateral staminodes often have small anther sacs that never contain any pollen. Because this small population may well consist of a single genotype, the presence of such an atavism in it may not be significant. On the other hand, the tendency for the medial antherode to be lacking, noted in the same population, is more important, because it has been found in all three Tana River District populations of subsp. *indehiscens* encountered, but not in any other populations of the species.

The lateral stamen filaments usually appear parallel. Commonly they are slightly bowed outward in the middle and converge again towards the apex (Figures 26*a*, 48*i*). Very rarely they may cross near the apex. The lateral anthers are generally held very close together.

The presence of two ovules in the dorsal locule of the ovary has been noted in two populations, both of subsp. *indehiscens*. Of the five examples that have been found, four had had only the basal seed develop while the fifth had had both ovules produce seeds. In the latter case these seeds were very similar to those of the ventral locules in size and shape. Three seeds were found in one ventral locule of a single capsule of *Faden & Faden 74/208* (subsp. *lilacinum*).

Hook-hairs have been noted on the ovary of a single flower of subsp. *indehiscens* (*Faden & Faden 74/380*) and on two of 13 capsules (one hook-hair on each) from cultivated plants of the same collection. Ovarian hook-hairs are otherwise unknown in this species.

Capsules of subsp. *indehiscens* are frequently indehiscent or only partly dehiscent along the lateral sutures. Occasionally the dorsal locule also splits for a short distance along the middorsal suture near the apex. Capsules of subsp. *lilacinum* seem to always dehisce along the lateral sutures but never along the middorsal suture. A specimen of subsp. *keniense* (*Faden et al. 70/894A*) appears to have regularly dehiscent capsules, while cultivated plants of another collection (*Faden & Faden 77/788*) have indehiscent capsules. The extent of dehiscence is difficult to determine in pressed specimens because their preparation often produces or increases the split.

Dorsal capsule valves are almost always persistent. In two

collections of subsp. *lilacinum* (*Compton 26824* and *Codd 6891*) and one of subsp. *keniense* (*Faden et al. 70/894A*), however, they appear to be regularly deciduous.

The three subspecies are allopatric (Map 11). Although subsp. *lilacinum* is geographically separated by almost 1500 km from the other two subspecies, few characters distinguish the three subspecies unequivocally. There is some evidence that the gap between subsp. *indehiscens* and subsp. *lilacinum* may be an artifact of inadequate collecting. Most of the intervening area between the known distributions is considered poorly or only moderately collected (A.E.T.F.A.T., 1965, "Map of the Extent of Florisitic Exploration of Africa South of the Sahara"). Furthermore, the two southernmost mainland collections of subsp. *indehiscens* show some morphological tendencies towards subsp. *lilacinum: Faulkner 4471* has more numerous uniseriate hairs on the bracteoles than any other collection of the subspecies; and *Faden & Faden 74/380* (from the same population) sometimes has petals with a faint pink tinge, at least in cultivation, a character otherwise unknown in subsp. *indehiscens*. This pattern suggests possible clinal variation between these subspecies.

Aneilema indehiscens is most closely related to *A. petersii* and *A. recurvatum*. Indeed it may prove to have arisen as an allopolyploid hybrid between the two. All three species have been found in the Kerio Valley of western Kenya and, at two of the four known localities for *A. indehiscens* subsp. *keniense*, it was found growing with *A. recurvatum*. In eastern Kenya subsp. *indehiscens* occurs not far from both subspecies of *A. petersii* but is ecologically distinct from each. Among the 13 populations of *A. indehiscens* subsp. *indehiscens* and 22 of *A. petersii* (both subspecies) observed in the field, only one instance has been found of the two species growing together. That was in a disturbed ecotonal situation in Tana River District (see Faden, 1983b). *Aneilema indehiscens* may be distinguished from *A. petersii* by the former's trailing habit, often falcate antherode lobes, usually slightly elongate connectives, lateral stamen filaments usually not crossing, narrower, often indehiscent capsules, and only slight dimorphism between dorsal and ventral locule seeds. From *A. recurvatum*, *A. indehiscens* differs by the latter's less symmetric, puberulous bracteoles that lack marginal glands, larger flowers with puberulous sepals, more rounded paired petals, less divergent and less strongly curved lateral stamen filaments that are usually not retained by the medial petal, and generally larger capsules that are often indehiscent.

3. *Aneilema recurvatum* Faden, new species

Aneilema rendlei sensu Chiovenda, Webbia, 8:38, 1951, pro *Corradi 2159*, p.p. [non Clarke, 1901].

Aneilema tacazzeanum sensu Lewis, Sida, 1:279, 1964 [non Hochstetter ex A. Richard, 1850 = *A. forskalii* Kunth].

Aneilema sp. C.—Faden in Agnew, Upland Kenya Wild Fl., 666, 667, 1974.

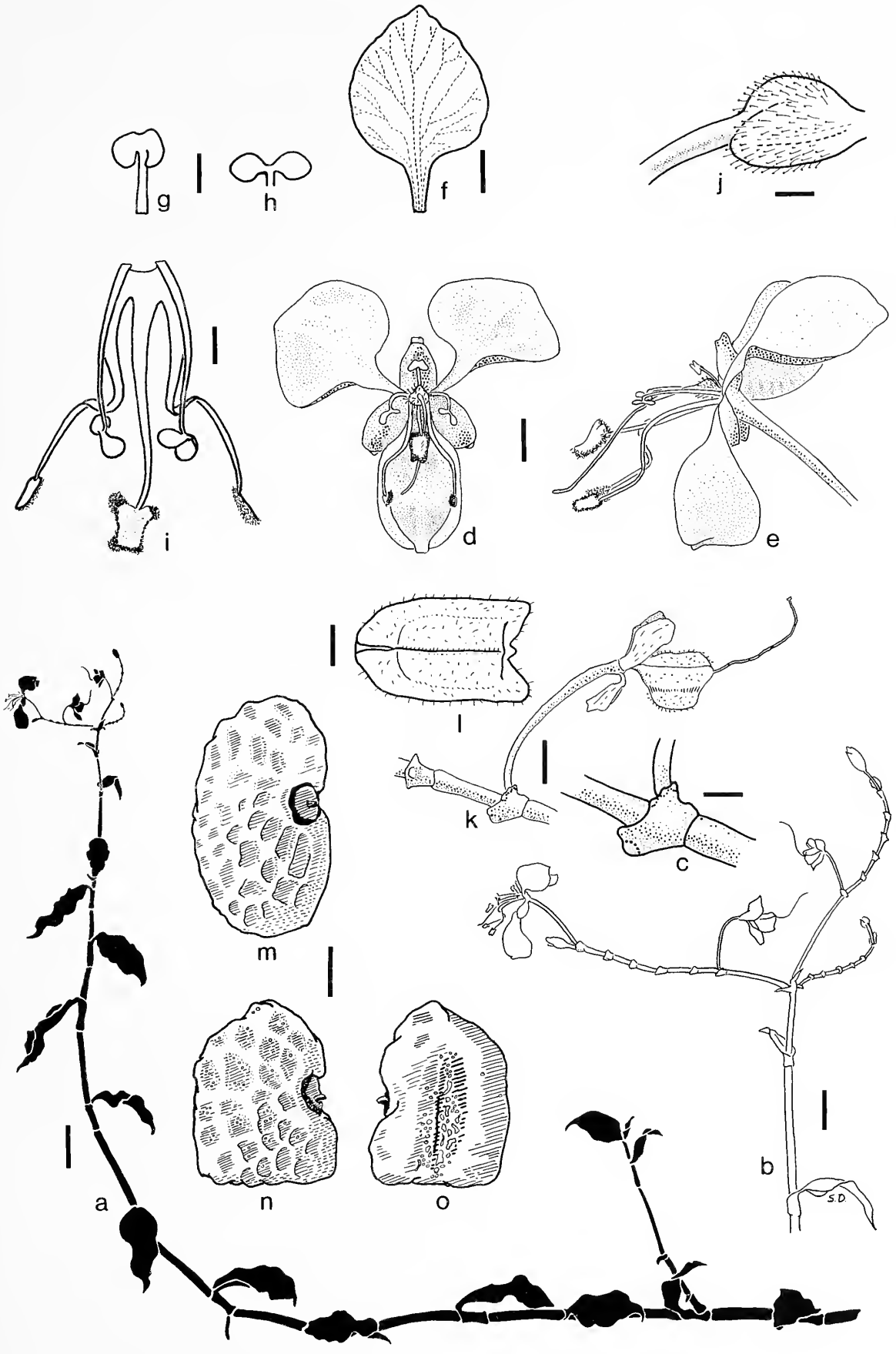
Herbae perennes foliis spiraliter dispositis laminis anguste lanceolato-ellipticis vel lanceolatis ad ovato-ellipticas, 2.5–7 (–8) cm longis, 0.5–2.2(–2.9) cm latis. Inflorescentiae thyrsi ovoidei ad late ovoideos, 2–4.5 cm longi, 2–6.5 cm lati, cincinnis (1–)2–7(–9) compositi. Bracteolae herbaceae, plus minusve symmetrice cupulatae perfoliatae, 1–2 mm longae, 0.5–1.25 mm altae, glandibus parvis marginalibus praeditae. Pedicelli 4.5–10 mm longi, tempore fructigero recurvati plerumque ~180°. Petala lilacina, medio calceolato stamina lateralia retinenti anthesis initio. Capsulae dehiscentes triloculares, (3–)3.5–5(–5.5) mm longae, 2–2.5 mm latae, loculo dorsali plerumque 1-seminali, loculis ventralibus uterque plerumque 2-seminalibus. Semina loculorum ventralium 1.4–2.3 mm longa, 1.25–1.6 mm lata, testis scrobiculatis (Figure 49).

TYPE.—Uganda, Bunyoro District, 23 mi N of Butiaba turnoff on Butiaba–Murchison Falls Nat. Park road, 6 mi N of Sambiye River crossing, near Kisansya, 16 Sep 1969, *Faden, Evans & Lye* [in *Faden*] *69/1066* (EA, sheet 1, holotype; BR, EA, sheet 2, K, MHU, isotypes; additional isotypes from material cultivated at the Missouri Botanical Garden, pressed 23 Jun 1973: MO, PRE, US).

Perennial herbs (habit types IA and IIA3, Figures 1, 2, 49*d*). Roots fibrous. Vegetative shoots decumbent to subscandent, profusely branched; flowering shoots ascending, sparsely branched, to 30 cm tall or more. Internodes (1–)2–12(–15) cm long, green, glabrous (rarely sparsely puberulous and glabrescent). Leaves spirally arranged, sheaths 0.5–1.5(–2) cm long, puberulous, ciliate at the apex, laminae shortly petiolate, gradually reduced towards the terminal inflorescence, narrowly lanceolate-elliptic or lanceolate to ovate-elliptic, 2.5–7(–8) cm long, 0.5–2.2(–2.9) cm wide, apex acuminate to acute, margin undulate, scabrid, occasionally also sparsely ciliate or ciliolate, both surfaces lustrous, sparsely puberulous, adaxial rarely also, with a few long, uniseriate hairs, abaxial with shorter, more numerous uniseriate hairs on the veins.

Inflorescences thyrses (Figure 49*b*), terminal on the main flowering shoots and frequently on axillary inflorescence-shoots from the inflorescence bract and upper leaves (occasionally also terminal on short or long shoots from the lower nodes), moderately lax, ovoid to broadly ovoid, 2–4.5 cm long, 2–6.5 cm wide (to 11 cm long and 15 cm wide in cultivation), with (1–)2–7(–9) cincinni, alternate, subopposite or subverticillate (usually with a mixture of arrangements within the thyrse), ascending. Peduncles (1.5–)2.5–5(–6.8) cm long (to 10.5 cm long in cultivation), puberulous. Inflorescence bract

FIGURE 49.—*Aneilema recurvatum* Faden, new species: *a*, habit; *b*, inflorescence; *c*, bracteole; *d*, perfect flower, front view; *e*, perfect flower, side view; *f*, lateral petal; *g*, medial staminode; *h*, antherode of lateral staminode; *i*, androecium, top view, medial staminode omitted, gynoecium removed; *j*, ovary and base of style, side view; *k*, capsule attached to cincinnus, side view; *l*, dorsal capsule valve, dorsal view; *m*, dorsal locule seed, dorsal view; *n*, ventral locule seed, dorsal view; *o*, ventral locule seed, ventral view (*a*, *b*, *m–o*, from *Faden & Faden 77/785*; *c–l*, from *Faden 69/1300*). (Bars = 20 mm for *a*; 5 mm for *b*; 2 mm for *d–f,k*; 1 mm for *c*, *g–i,l*; 0.67 mm for *j*; 0.5 mm for *m–o*.)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supramedial (occasionally medial), usually herbaceous, foliaceous or bract-like. Inflorescence axis puberulous. Cincinni to 4.2 cm long and 15-flowered (to 10 cm long and 33-flowered in cultivation). Cincinnus bracts (rarely caducous) membranous (rarely the lowermost herbaceous), ascending to patent (rarely reflexed), ovate-elliptic or ovate-lanceolate to ovate or lanceolate (rarely the lowermost linear), 1.5–3(–9.5) mm long, glandular subapically, usually glabrous or subglabrous. Cincinnus peduncles generally ± uniform within the inflorescence and exceeding the cincinnus bracts, (1.1–)3–10.5(–12) mm long, puberulous. Cincinnus axis puberulous. Bracteoles attached (0.8–)1–4(–5) mm apart, herbaceous, ± symmetrically cup-shaped, perfoliate, 1–2 mm long, 0.5–1.25 mm high, prominently glandular subapically and with smaller, inconspicuous glands along the margin, glabrous (occasionally a few hairs near the base, very rarely 1–2 uniseriate hairs at the apex or along the fused edge) (Figure 49*c*).

Flowers perfect and staminate, odorless, 10–14 mm wide (Figure 49*d,e;* Plate 3*c,d*). Pedicels (4.4–)5–8(–9) mm long in flower, to 10 mm long in fruit, ascending in flower, in fruit recurved generally ~180°, either ± uniformly or mostly at base and apex, persistent, puberulous apically, otherwise glabrous (Figure 49*k*). Sepals prominently glandular near the apex; medial sepal elliptic to ovate-elliptic or ovate, 2.4–3(–3.5) mm long, 1.8–2.3 mm wide, usually glabrous (occasionally with a few hairs at the base), subapical gland distinctly bilobed, rarely smaller marginal glands also present; lateral sepals broadly elliptic to obovate-elliptic, oblong-elliptic, or ovate-elliptic, 2.5–3.5(–3.8) mm long, 1.6–2.4 mm wide, usually sparsely puberulous basally or medially (occasionally glabrous), subapical gland bilobed or unlobed, marginal glands absent. Paired petals 6.5–9(–11) mm long, 4–6.5(–7.5) mm wide (Figure 49*f*), limb ovate, 4.5–6.5(–7) mm long, lilac (RHS color: 85C-D and D, *Faden & Faden 77/785,* cultivated; 85C-D *Faden & Faden 77/786,* cultivated; 87D, *Faden et al.* [in *Faden*] *69/1066,* cultivated), apex acute to obtuse, margin crenulate, claw 1.5–3(–4) mm long, whitish, glabrous. Medial petal slipper-shaped, elliptic, broadest below the margin (viewed from the apex) (Figure 23*g–i*), retaining the lateral stamens when the flower opens (Plate 3*c*), 5–7.5(–8.5) mm long, 3–4(–4.8) mm wide, 3.2–4.3(–5) mm deep, concolorous with the limbs of the paired petals laterally, whitish medially. Lateral stamen filaments fused basally to medial stamen filament and sometimes to lateral staminode filaments (Figures 26*d,* 49*i*). Medial staminode with filament 1.4–2.3(–3) mm long, pale lilac basally, shading to yellow near the apex, antherode bilobed, yellow, lobes sessile or subsessile, obovate-cuneate to transversely elliptic, 0.3–0.65 mm long, connective not or scarcely elongate (Figure 49*g*). Lateral staminodes with filaments 3–4.8 mm long, very pale lilac shading to yellow above the middle, antherodes bilobed, yellow, lobes sessile or subsessile, obovate-cuneate, sometimes slightly decurved, 0.5–1 mm long, connective not elongate (Figure 49*h*). Lateral stamens with filaments slightly divergent in basal 1/3, strongly divergent in middle 1/3, less strongly divergent in apical 1/3 (Figures 26*d,* 49*i*), 6.2–8.6 mm long, S-shaped, geniculate, glabrous, anthers lanceolate to elliptic (to ovate), 0.8–1.2 mm long, 0.5–0.9 mm wide, pollen yellow. Medial stamen with filament 4.2–6 mm long, anther ovate-elliptic to oblong-elliptic, saddle-shaped, 1.5–2.2 mm long, 0.95–1.4 mm wide, pollen concolorous with lateral anther pollen. Ovary substipitate, obovate to obovate-oblong or obovate-subquadrate, 1.3–1.8 mm long, 0.9–1.45 mm wide, densely and uniformly covered with patent, glandular hairs (Figures 42*k,* 49*j*), apex emarginate, dorsal locule prominent, 1-ovulate, ventral locules each 2-ovulate; style 7–8.5 mm long, straight to gently arcuate-decurved for most of its length, also curved laterally out of the floral midplane, stigma capitate, held in front of the anthers and about the same level as the lateral anthers.

Capsules (Figure 49*k,l*) substipitate or subsessile, oblong-elliptic to obovate-oblong (occasionally obovate), dehiscent, bivalved, trilocular, (3–)3.5–5(–5.5) mm long, 2–2.5 mm wide, pale gray to grayish tan, lustrous, puberulous, apex emarginate, valves persistent or dorsal valve tardily deciduous (occasionally both valves deciduous in old capsules), dorsal locule prominent, 1-seeded or, by abortion, empty, ventral locules each 2-(or, by abortion, 1-)seeded, cells of the capsule wall transversely elongate. Dorsal locule seed (Figure 49*m;* Plate 6*c*) elliptic to oblong-elliptic, 1.9–2.6 mm long, 1.25–1.45 mm wide, 0.75–09 mm thick, hilum dark brown, usually in a very shallow groove, much shorter than the seed, testa brown, shallowly scrobiculate or with shallow pits radiating from the embryotega on the dorsal surface, white (rarely gray) farinose granules sparse in the depressions and around the embryotega, usually dense around the hilum, hypha-like filaments occasionally present among the farinose granules; ventral locule seeds (Figure 49*n,o;* Plate 6*c*) ovate to trapezoidal, apical seed rounded to obtuse apically, basal seed angular (rarely obtuse) basally, 1.4–2.3 mm long, 1.25–1.6 mm wide, 0.7–0.9 mm thick, hilum dark brown, raised in a groove, not extended onto apical and basal surfaces, testa brown, shallowly scrobiculate or with shallow pits radiating from the embryotega on the dorsal surface, white (rarely gray) farinose granules sparse in the depressions (more abundant than in dorsal locule seed depressions), usually sparse around the embryotega, dense around the hilum, hypha-like filaments occasionally present among the farinose granules.

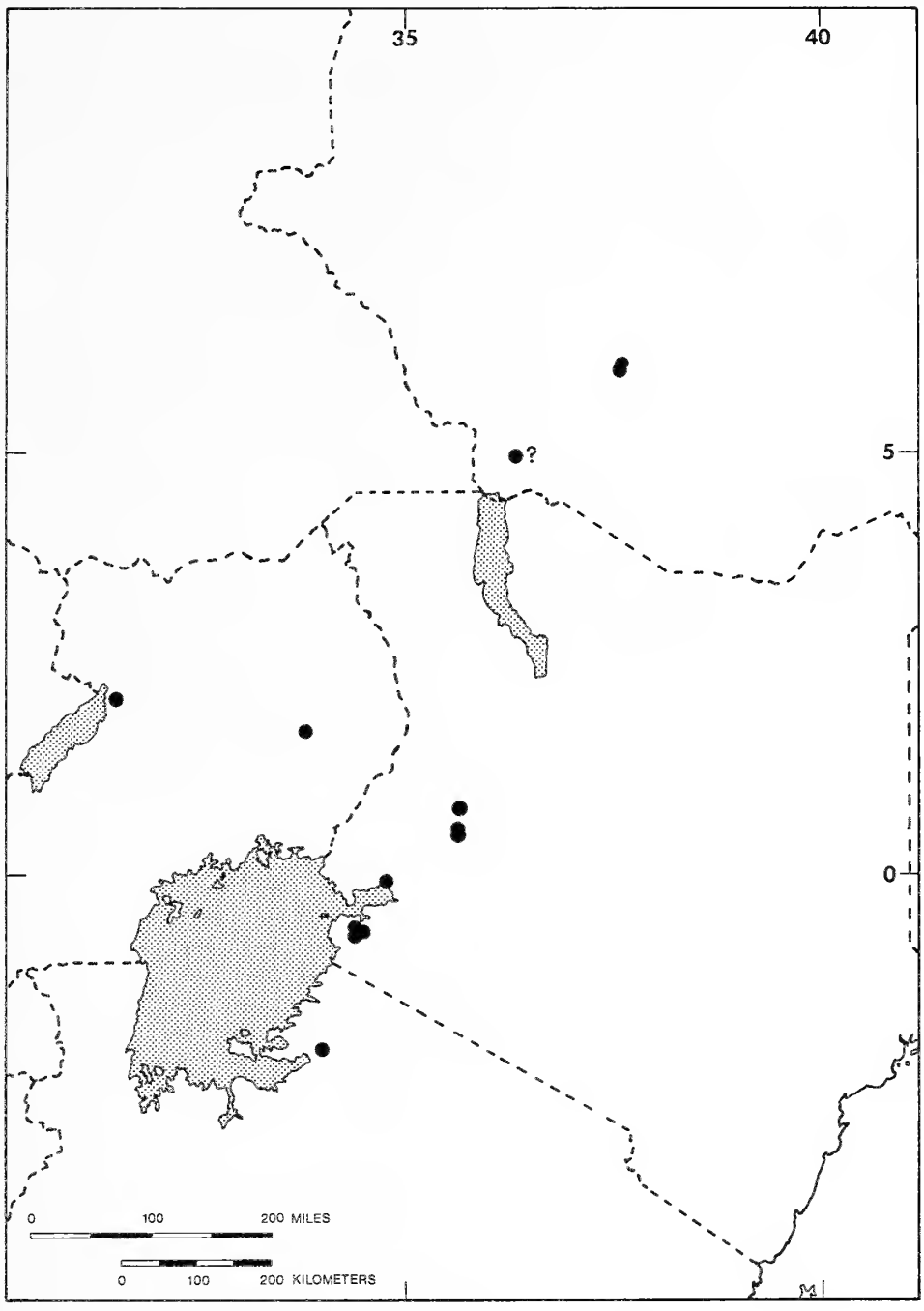
HABITAT.—Grassland, bushland, and bushland thickets, sometimes near streams; sandy or clayey soils; partial shade; 700–1300 m.

FLOWERING.—Flowering specimens have been seen from March, April, and July–November. In cultivation, the flowers of two populations open at the same time as those of three populations of *A. clarkei,* which is equivalent to a field time of about 0900 hrs. The flowers of one of the *A. recurvatum* populations fade at an equivalent time of 1345 hrs.

CHROMOSOME NUMBER.—$n = 13$, $2n = 26$.

DISTRIBUTION.—SE Ethiopia, N Uganda, W Kenya, and NW Tanzania (Map 12).

SPECIMENS SEEN.—ETHIOPIA. GEMU-GOFA: Rive del



MAP 12.— Distribution of *Aneilema recurvatum* Faden, new species.

Ghizo, *Corradi 2159*, p.p. (FT); base of escarpment W of Arba Minch, 6°00′N, 37°35′E, *Gilbert & Gilbert 1617* (EA, K); Arba Minch, below escarpment E of town ~6°05′N, 37°37′E, *Gilbert & Thulin 318* (MO); Arba Minch, cultivated in Addis Ababa, *Mistry M-11A* (EA) & *M-27* (EA).

UGANDA. BUNYORO: 23 mi N of Butiaba turn off on Butiaba–Murchison Falls Nat. Park road, 6 mi N of Sambiye River crossing, near Kisansya, *Faden et al.* [in *Faden*] *69/1066* (BR, EA—2 sheets, K, MHU); same collection, cultivated Missouri Botanical Garden (MO, PRE, US); near Kisansya on Butiaba Flats, 2°10′N, 31°24′E, *Lye et al. 3981* (K). TESO: 1.8 mi W of Wera, *Lewis 5999* (K, MO).

KENYA. Without locality, *Graham 3019* (K). ELGEYO: Kerio Valley, Kabarnet–Tambach road, 2.8 km before junction with Tot road, 0°32′N, 35°35′E, *Faden & Faden 77/785* (DSM, EA, F, K, MO, US); Tambach–Tot road, Toilang, ~0°53′N,

35°37′E, *Faden & Faden 77/786* (EA, F, K, US); Tambach–Tot road, 10 km N of junction with Kabarnet–Tambach road, 0°37′N, 35°36′E, *Faden et al. 70/894* (BR, EA, K, MO, US). KISUMU-LONDIANI: Kisumu, *Hindorf 806* (EA). SOUTH KAVIRONDO: Lambwe Valley, Riamkanga, 0°42′30′S, 34°12′E, *Faden 69/1300* (BR, EA, FT, K, MO, PRE); same collection, cultivated Missouri Botanical Garden (B, C, DSM, G, P, UPS, S, US, WAG); Lambwe Valley, Ruma thicket, ~0°37′S, 34°18′E, *Faden 69/1608* (EA); Lambwe Valley, between Otuok and Ruma thickets, ~0°39′S, 34°17′E, *Faden 69/1642* (EA, MO); Lambwe Valley, Got Jope, W slope, 0°34′S, 34°19′E, *Faden 69/1699* (EA, K); Lambwe Valley, E side of small hill E of Got Rabondo, ~0°41′S, 34°13′E, *Faden 69/1802* (EA, K); Wiga Valley, ~0°40′S, 34°12′E, *Faden 69/1933* (EA, FT, K, MO); Lambwe Valley near River, *Napier & Fox 3431* [= *6821*] (EA, K).

TANZANIA. MUSOMA: Ushashi Rest House, Ushashi, *Tanner 4011* (BR—2 sheets, K).

DISCUSSION

Corradi 2159, which is a mixed collection with *A. rendlei* C.B. Clarke, has been doubtfully included in *A. recurvatum.* It differs from typical specimens in having more densely pubescent leaves, more patent cincinni, more regularly reflexed cincinnus bracts, shorter cincinnus peduncles, and less widely spaced bracteoles. An apparently mature flower bud was dissected on *Corradi 2159* and showed larger antherode lobes on the lateral staminodes and much less curled lateral stamen filaments than buds of typical *A. recurvatum* plants. *Corradi 2159* agrees with *A. recurvatum* in the form, size, and lack of pubescence of the bracteoles and in the pubescence of the cincinni, pedicels, and sepals. Although aberrant in many characters, *Corradi 2159* is closer to *A. recurvatum* than to any other species of section *Lamprodithyros.* However, since it lacks flowers and capsules, a final decision about its taxonomic status must await the collection of better material.

Both *Faden 69/1300* and *Faden et al. 70/894* are mixed collections with *A. indehiscens* subsp. *keniense* (*69/1300A* and *70/894A* respectively). Their distinctions from the more abundant material of *A. recurvatum* are discussed under *A. indehiscens.*

Aneilema recurvatum approaches *A. indehiscens* in habit; however, the long, trailing shoots of the former tend to be much more branched than those of the latter. The differences are maintained in cultivation.

The stamen-retention mechanism is well developed in *A. recurvatum* (Plate 3*c,d*). In cultivated plants the stamens are held by the medial petal for about one to two hours.

Aneilema recurvatum is very common in the Lambwe Valley of southwestern Kenya, where it occurs at the edges of moist thickets composed of a variety of trees and shrubs, including *Mystroxylon aethiopicum, Euphorbia candelabrum, Scutia myrtina, Erythroxylum fischeri,* and species of *Cadaba, Euclea, Grewia, Rhus,* and *Scolopia.* In the Kerio Valley of western Kenya, it occurs in drier thickets with *Acacia mellifera, A. brevispica, Teclea pilosa, Grewia* sp., *Sansevieria ehrenbergii,* and *Cissus rotundifolia.*

Aneilema recurvatum is a distinctive species because of its nearly symmetric, glabrous bracteoles, narrow, pointed paired petals, and small capsules and seeds. It appears to be most closely related to *A. forskalii, A. sebitense,* and *A. benadirense* because of the form of its bracteoles and their marginal glands and lack of pubescence. It differs from *A. forskalii* by its perennial habit, less-widely spaced bracteoles, smaller, less-obovate, more shortly stipitate to subsessile capsules and smaller seeds. From *A. sebitense A. recurvatum* may be separated by the latter's glabrous or glabrescent internodes, more recurved fruiting pedicels that are puberulous at the apex, smaller capsules with never more than two seeds per ventral locule, and smaller dorsal locule seeds. *Aneilema recurvatum* differs from *A. benadirense* by the former's more regularly ascending cincinni, which are fewer per thyrse, generally less-recurved fruiting pedicels, well-developed medial staminode, and less-humpbacked ventral capsule valve. It further differs from all three species in its less dimorphic dorsal and ventral locule seeds.

Aneilema recurvatum can be confused with *A. indehiscens* and *A. petersii* but is easily separated by its more symmetric, glabrous bracteoles that are always perfoliate. It can also be distinguished by its glabrous or subglabrous sepals, more pointed paired petals, well-developed stamen-retention habit, more dimorphic antherodes, more divergent lateral stamen filaments, and generally smaller capsules. Its more or less uniformly colored capsules are paler than those of *A. indehiscens.* Its seeds are much less dimorphic and smaller than those of *A. petersii.*

4. *Aneilema sebitense* Faden, new species

Aneilema rendlei C.B. Clarke, Fl. Trop. Africa, 8:69, 1901 [pro *Donaldson Smith 346*].

Herbae perennes foliis spiraliter dispositis laminis lanceolato-ellipticis ad lanceolatas, ovato-lanceolatas vel ovatas, 3–13.5 cm longis, (0.7–)1.5–4 cm latis, margine ciliata. Inflorescentiae thyrsi ovoidei ad late ovoideos, 4–10 cm longi, 3.5–10 cm lati, cincinnis (2–)5–9(–12) compositi. Bracteolae 2–5(–6.2) mm semotae, plus minusve herbaceae, plus minusve symmetrice cupulatae perfoliatae, glabrae, glandibus numerosis marginalibus praeditae. Pedicelli tempore fructigero plerumque ascendentes vel erecti, glabri. Capsulae, stipitatae, dehiscentes, (4–)4.5–7.5 mm longae, (2.3–)2.8–3.5(–3.7) mm latae, loculo dorsali 1-seminali, loculis ventralibus uterque plerumque 2–3(–4)-seminalibus. Semen loculi dorsalis 2.15–2.85 mm longum, 1.5–1.7 mm latum, 1–1.2 mm crassum. Semina loculorum ventralium (1.35–)1.5–2(–2.9) mm longa, 1.55–1.9(–2) mm lata (Figure 50).

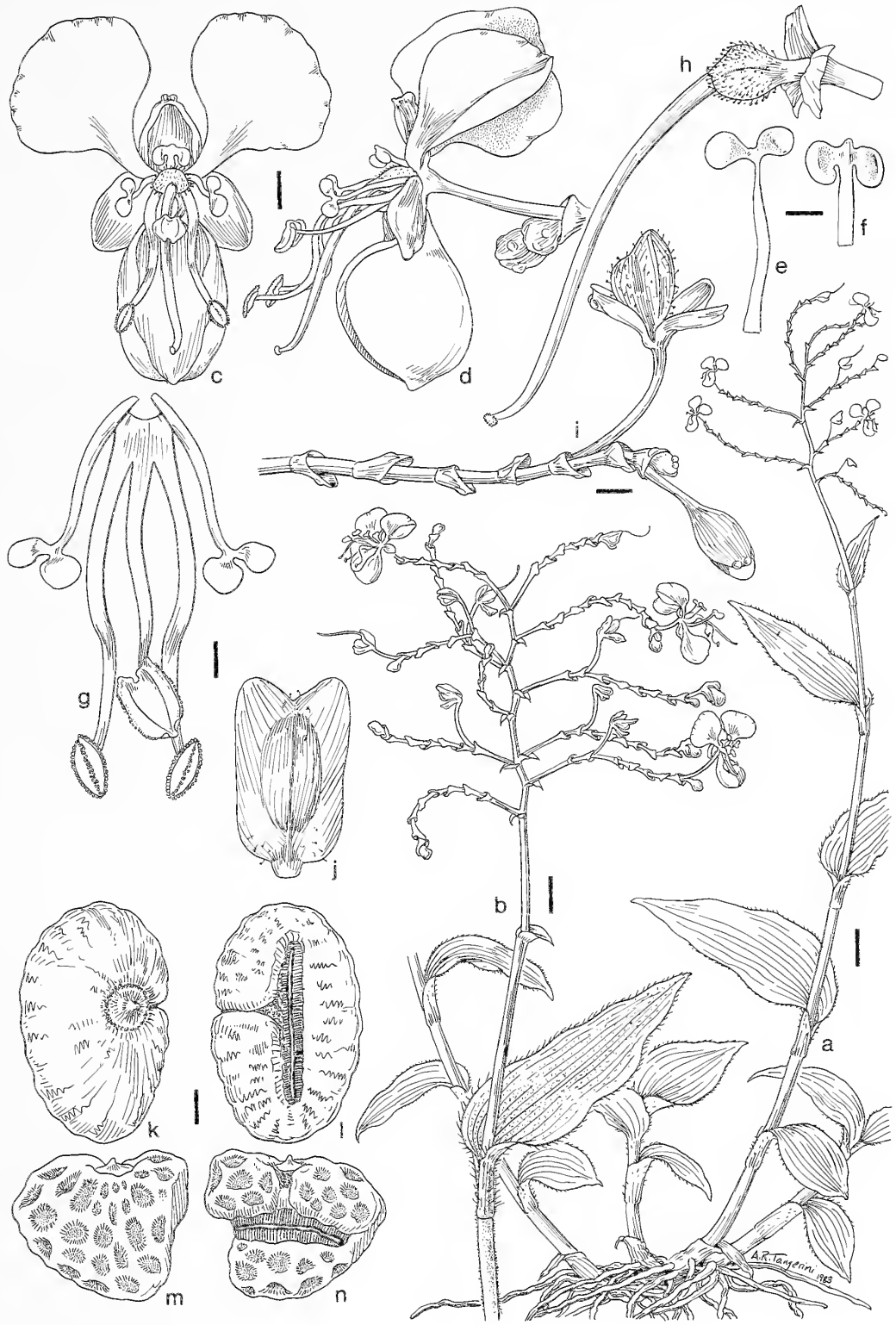


FIGURE 50.—*Aneilema sebitense* Faden, new species: *a*, habit; *b*, inflorescence; *c*, perfect flower, front view; *d*, perfect flower, side view; *e*, lateral staminode; *f*, medial staminode; *g*, androecium, top view, medial staminode omitted, gynoecium removed; *h*, gynoecium, side view; *i*, capsule attached to cincinnus, side view; *j*, dorsal capsule valve, dorsal view; *k*, dorsal locule seed, dorsal view; *l*, dorsal locule seed, ventral view; *m*, ventral locule seed, dorsal view; *n*, ventral locule seed, ventral view (all from *Faden & Faden 77/803*). (Bars = 20 mm for *a;* 10 mm for *b;* 2 mm for *c,d,i;* 1 mm for *e-h, j;* 0.4 mm for *k-n.*)

TYPE.—Kenya, West Suk District (West Pokot District on label), near Sebit on Sebit-Parua road, along Sebit River, 1°24′N, 35°22′E, 15 Mar 1977, *Faden & Faden 77/803*, field collections and specimens pressed from cultivation 27 Sep 1977 and other dates (US, holotype; BR, EA, F, K, MO, P, US, WAG, isotypes).

Perennial herbs (habit types IB, IC, Figures 1, 50*a*). Roots fibrous. Shoots ascending, sometimes rooting at the lower nodes, to ~1 m tall. Internodes 1.5–16.5 cm long, puberulous. Leaves spirally arranged, sheaths 1–2.5 cm long, pilose-puberulous, ciliate at the apex, laminae petiolate (except the uppermost leaves), sometimes reduced towards the inflorescence, lanceolate-elliptic to lanceolate, ovate-elliptic or ovate, 3–13.5 cm long, (0.7–)1.5–4 cm wide, apex acuminate to acute, margin slightly undulate, scabrid, also ciliate at least below the middle and on the petiole, both surfaces ± dull, densely puberulous, sometimes also with scattered uniseriate hairs, those of the adaxial surface longer than those of the abaxial.

Inflorescences thyrses, terminal and sometimes axillary from the inflorescence bract, lax to moderately lax, ovoid to broadly ovoid, 4–10 cm long, 3.5–10 cm wide, with (2–)5–9(–12) cincinni, ascending (occasionally the lower becoming declinate), alternate or a few subopposite (Figure 50*b*). Peduncles (3–)5–13 cm long, puberulous. Inflorescence bract usually medial, occasionally supramedial, membranous and bract-like or herbaceous and foliaceous. Inflorescence axis glabrous to sparsely puberulous (at least basally). Cincinni to 5 cm long and 13-flowered (to 6 cm long in cultivation). Cincinnus bracts membranous, appressed to the cincinnus peduncles or patent, ovate-elliptic to ovate or lanceolate, 2–3(–5) mm long, at least the upper ones glandular subapically but marginal glands lacking, glabrous or occasionally sparsely puberulous. Cincinnus peduncles relatively uniform within the inflorescence, exceeding the cincinnus bracts, 5–10(–14) mm long, usually glabrous, occasionally sparsely puberulous. Cincinnus axes usually glabrous, occasionally puberulous. Bracteoles attached 2–5(–6.2) mm apart (to 8 mm apart in cultivation), ± herbaceous, nearly symmetrically cup-shaped, perfoliate, 1.8–2.7 mm long, 1–1.6 mm high, prominently glandular subapically and with numerous smaller glands along the margin, glabrous.

Flowers perfect and staminate, odorless, 10–20 mm wide (Figure 50*c,d;* Plate 3*e*). Pedicels 6.5–10.5 mm long in flower, to 13 mm long in fruit, ascending in flower, ascending to erect or very slightly further recurved in fruit, persistent, glabrous (Figure 50*i*). Sepals glandular near the apex, glabrous; medial sepal ovate-elliptic to ovate-lanceolate, 3.5–4.4(–6) mm long, 2.2–2.9 mm wide, gland bilobed; lateral sepals broadly elliptic, obovate-elliptic or oblong-elliptic to obovate-oblong or ovate-lanceolate, 3.5–4.5(–6) mm long, 1.9–3.5 mm wide, gland unlobed or bilobed. Paired petals 9–10.5 mm long, 6–10 mm wide, limb ovate, 7–8 mm long, lilac (RHS colors: 81D, *Faden & Faden 77/803,* cultivated; 82D, *Faden & Faden 77/803A,* cultivated), apex obtuse or rounded to acute, claw 2–3 mm long, white basally, glabrous. Medial petal cup-shaped, elliptic to obovate, broadest just below the margin (viewed from the apex), retaining the lateral stamens when the flower opens, 7.5–13 mm long, 5.5–8 mm wide, 5–7 mm deep, concolorous with the limbs of the paired petals or slightly paler (Figure 50*c,d*). Stamen filaments shortly fused basally, sometimes also fused with the lateral staminodes (Figure 50*g*). Medial staminode with filament 1.7–3 mm long, white or pale lilac shading to yellow above the middle, antherode bilobed, yellow, lobes sessile, transversely elliptic to reniform, 0.4–1 mm long, connective slightly elongate (Figure 50*f*). Lateral staminodes with filaments 4–5 mm long, white or pale lilac shading to yellow near the apex, antherodes bilobed, yellow, lobes stipitate or sessile, broadly ovate-reniform to obovate, 0.5–1 mm long, connective not at all to scarcely elongate (Figure 50*e*). Lateral stamens with filaments parallel to divergent (Figure 50*g*), 8.7–11.5 mm long, S-shaped, geniculate and decurved near the middle, glabrous, anthers ovate-elliptic to lanceolate-elliptic, 1.1–1.6 mm long, 0.5–1 mm wide, pollen creamy yellow to dirty white. Medial stamen with filament 6–7.5 mm long, anther ovate to lanceolate-ovate or oblong-elliptic, saddle-shaped, 1.7–2.5 mm long, 0.9–1.5 mm wide, pollen golden yellow. Ovary substipitate, obovate to obovate-oblong, ~2 mm long, 1.3–1.5 mm wide, densely and uniformly covered with patent, glandular hairs, apex truncate, dorsal locule prominent, 1-ovulate, ventral locules each 2–3(–4?)-ovulate; style ~10.5 mm long, arcuate-decurved for most of its length, also slightly curved laterally, stigma capitate, usually held in front of the lateral anthers (Plate 3*e*).

Capsules (Figure 50*i,j*) stipitate, obovate-oblong to obovate, oblong, oblong-elliptic or obovate-elliptic, dehiscent, bivalved, trilocular, (4–)4.5–7.5 mm long, (2.3–)2.8–3.5(–3.7) mm wide, tan or grayish tan, sometimes marked with blue apically or flecked with dark brown spots, lustrous, puberulous to subglabrous, apex emarginate to rarely subtruncate, dorsal valve deciduous, dorsal locule prominent, 1-seeded or, by abortion, empty, ventral locules each 2–3(–4) seeded, sometimes (in cultivation), by abortion, 1-seeded; cells of the capsule wall transversely elongate, arranged in regular files. Dorsal locule seed (Figure 50*k,l*) not or scarcely humpbacked towards the capsule apex, elliptic, 2.15–2.85 mm long, 1.5–1.7 mm wide, 1–1.2 mm thick, hilum dark brown, in a shallow groove, shorter than the seed, testa buff or buff-orange, very shallowly reticulate or scrobiculate to ± smooth, brownish farinose granules very sparse in the depressions and more abundant around the hilum or confined to the hilum, hypha-like filaments very sparse in the depressions or absent. Ventral locule seeds (Figure 50*m,n*) ovate to trapezoidal, apical seed rounded to obtuse apically, basal seed angular basally, (1.35–)1.5–2(–2.9) mm long, 1.55–1.9(–2) mm wide, 1–1.25 mm thick, hilum dark brown, raised in a groove, not or slightly extended onto apical and basal surfaces, testa tan or yellowish brown, shallowly reticulate to reticulate-scrobiculate, brownish

farinose granules sparse in the depressions and around the embryotega, dense around the hilum, hypha-like filaments occasional or frequent in the depressions.

HABITAT.—*Acacia-Commiphora-Combretum* woodland and dry hillsides above river; rocky areas; ~1120–1550 m.

FLOWERING.—Flowering specimens have been seen from April, July, and August. In cultivation, the two Faden and Faden collections and *Gilbert & Thulin 266* flower early in the morning (before *A. recurvatum*), but the exact hours have not been determined.

CHROMOSOME.—$2n = 52$.

DISTRIBUTION.—SW Ethiopia and NW Kenya (Map 10).

SPECIMENS SEEN.—ETHIOPIA. GEMU-GOFA: Arba Minch, escarpment below the town, ~6°05′N, 37°35′E, *Gilbert & Thulin 266* (MO). SIDAMO: ["Somali-land" on label], *Donaldson Smith 346* (BM).

KENYA. WEST SUK: Near Sebit on Sebit-Parua road, along Sebit River, 1°24′N, 35°22′E, *Faden & Faden 77/803* (BR, EA, F, K, MO, P, US, WAG); same locality, *Faden & Faden 77/803A* (F, US); Cherangani Hills, R. Sebit, 1°12′N [sic: changed to 1°24′N on EA sheet], 35°19′E, *Mabberley & McCall 88* (EA) and *88a* (K) [part of same collection according to Mabberley (in litt.)].

DISCUSSION

Donaldson Smith collected his number 346 on 23 April 1895, the same day as he collected the type of *Aneilema rendlei*. The locality is in Ethiopia (foot of the Amaro Mountains, Burga Camp) not in the Somali Republic, according to the collector's account of his journey (Donaldson Smith, 1897). Clarke (1901) treated this specimen as *A. rendlei* but noted that it could hardly be distinguished from the Australian *A. acuminatum*. The resemblance to the latter is purely superficial. For distinctions from *A. rendlei* see discussion under that species.

In Faden (1975:289) I treated this as a species apparently distinct from but closely related to *A. forskalii*. The inadequacy of the four herbarium specimens then available dissuaded me from formally describing this species. The living material subsequently obtained of both *A. forskalii* and *A. sebitense* has confirmed my original conclusion.

Aneilema sebitense resembles *A. forskalii* in its bracteoles relatively widely spaced, more or less symmetrically cup-shaped, glabrous, and with numerous marginal glands, fruiting pedicels mostly erect, and fruits commonly with more than two seeds per ventral locule. It differs from *A. forskalii* by its perennial habit, ciliate leaf margins, generally less widely spaced bracteoles, narrower, more shortly stipitate capsules with up to four seeds per ventral locule, and smaller seeds. In addition, the petals of *A. sebitense* seem to be darker in color and the antherodes of the lateral staminodes different in shape than those of *A. forskalii*.

Aneilema sebitense also resembles *A. recurvatum* but can be distinguished by its glabrous pedicels that are generally less reflexed in fruit, less-divergent lateral stamen filaments, and larger capsules with larger seeds that are more dimorphic.

Living plants of *Faden & Faden 77/803* are much larger, more robust, and have much larger flowers than those of *Gilbert & Thulin 266*. Their flowers also differ in details of color and the shape of some parts. I initially thought that these populations might be worth separating at some taxonomic level, but they agree in all diagnostic characters, and both populations proved to be tetraploid.

5. *Aneilema forskalii* Kunth

Aneilema forskalii Kunth ["Anilema Forskâlei"], Enum. Pl., 4:71, 1843.—C.B. Clarke in De Candolle, Monogr. Phan., 3:231, 1881.—Schweinfurth, Bull. Herb. Boissier, 1, append., 2:58, 1894. [Type as for *Commelina tuberosa* Forsskål.]

Commelina tuberosa Forsskål, Fl. Aegypt.-Arab. Descript., 12, 1775 [nom. illeg., non L. (1753). Syntypes: Arabia felix [Yemen], Montes Hadienses ad Bulgliose, Mar 1763, *Forsskål in Herb. Forskalii 33* (C, lectotype; photo K, MO, US), *in Herb. Forskalii 31* (C, photo US) and *in Herb. Forskalii 32* (C; photo K, MO, US)].

Commelina paniculata Vahl, Enum. Pl., 2:179, 1805-1806 [nom. illeg., non Hill (1773)].—Roemer and Schultes, Syst. Veg., 1:538, 1817. [Type as for *Commelina tuberosa* Forsskål.]

Aneilema tacazzeanum Hochstetter ex A. Richard, Tent. Fl. Abyssinicae, 3(5):343, 1850 ["tacazzeana"].—Walpers, Ann. Bot. Syst., 3:658, 1852.—Hua, Bull. Mus. Hist. Nat. (Paris), 1:120, 1895 [in adnot. sub *Aneilema aequinoctiale*].—Schumann in Engler, Pflanzenwelt Ost-Afrikas C, 136, 1895.—Andrews, Fl. Pl. Sudan, 3:239, 1956.—Brenan, Kew Bull., 15:215, 1961.—Cufodontis, Bull. Jard. Bot. Natl. Belgique, 41, suppl., 1518, 1971. [Syntypes: Ethiopia, bords du Tacazzé [undated]), *Quartin Dillon & Petit s.n.* (P—2 sheets; photo EA, K; lectotype: P sheet ex Herbarium Richard); Valle fluvii Tacaze, prope Dscheladscheranne [Djeladjeranne; cited by Richard as "Tchélatchékanné,"] *Schimper 1660* (G—2 sheets, K—2 sheets, MO, P—3 sheets, photo EA).]

Lamprodithyros tacazzeanus (Hochstetter ex A. Richard) Hasskarl, Flora, 46:390, 1863; in Peters, Naturwiss. Reise Mossambique, Bot., 531, 1864 [nom. tant., desc. et *Peters s.n.* excl.].

Lamprodithyros ehrenbergii Hasskarl in Schweinfurth, Beitr. Fl. Aethiop., 210, 1867. [Type: Ethiopia, Togodele, 1822, *Ehrenberg 413* (B; photo K, fragment L).]

Commelina ebracteata Ehrenberg, in sched. (*Ehrenberg 413*).—Hasskarl in Schweinfurth, Beitr. Fl. Aethiop., 210, 1867 [pro syn.].

Aneilema ehrenbergii (Hasskarl) C.B. Clarke in De Candolle, Monogr. Phan., 3:229, 1881 [*Welwitsch 6610* excl.]; in Thiselton-Dyer, Fl. Trop. Africa, 8:74, 1901.—Durand and Schinz, Conspect. Fl. Africae, 5:430, 1895.—Cufodontis, Bull. Jard. Bot. Natl. Belgique, 41, suppl., 1517, 1971.

Aneilema tacazzeanum Hochstetter ex C.B. Clarke in De Candolle, Monogr. Phan., 3:222, 1881; in Thiselton-Dyer, Fl. Trop. Africa, 8:66, 1901.—Durand and Schinz, Conspect. Fl. Africae, 5:132, 1895.—Täckolm and Drar, Fl. Egypt, 2:433, 1950. [Syntypes: Ethiopia, *Schimper 1660*, p.p. maj. [fide Clarke, 1881] (G, P); *Schimper 1729* (G, K, P); Oudgerade, *Petit s.n.* (P, not seen); Mozambique, *Peters s.n.* (B, destroyed, fragment L).]

Aneilema aequinoctiale (P. de Beauvois) G. Don β *minor* C.B. Clarke in De Candolle, Monogr. Phan., 3:221, 1881.—Durand and Schinz, Conspect. Fl. Africae, 5:429, 1895. [Syntypes: Ethiopia, *Schimper 1660*, p.p. [fide Clarke] (P); *Quartin Dillon* [*& Petit*] *s.n.* (P); Yemen, *Botta s.n.* (P).]

Annual herbs (habit types IB?, IC, IIIA, IIIB, Figure 1). Roots fibrous. Shoots erect to ascending or shortly decumbent,

unbranched or sparsely branched, 20–50(–70) cm tall. Internodes (0.5–)2.5–12(–19) cm long, sparsely to densely puberulous. Leaves spirally arranged, sheaths 0.5–1.5(–2) cm long, pilose-puberulous (occasionally puberulous), ciliate at the apex, laminae petiolate, sometimes gradually reduced towards the inflorescences, mostly lanceolate-elliptic to ovate-elliptic (occasionally lanceolate or ovate), 2.5–12 cm long, (0.5–) 1.3–4.5 cm wide, apex acute to acuminate, margin usually planar (occasionally slightly undulate), scabrid, occasionally also sparsely ciliolate, ciliate on the petiole, both surfaces puberulous, adaxial also generally with scattered, long, uniseriate hairs, abaxial often with numerous, shorter uniseriate hairs on the veins.

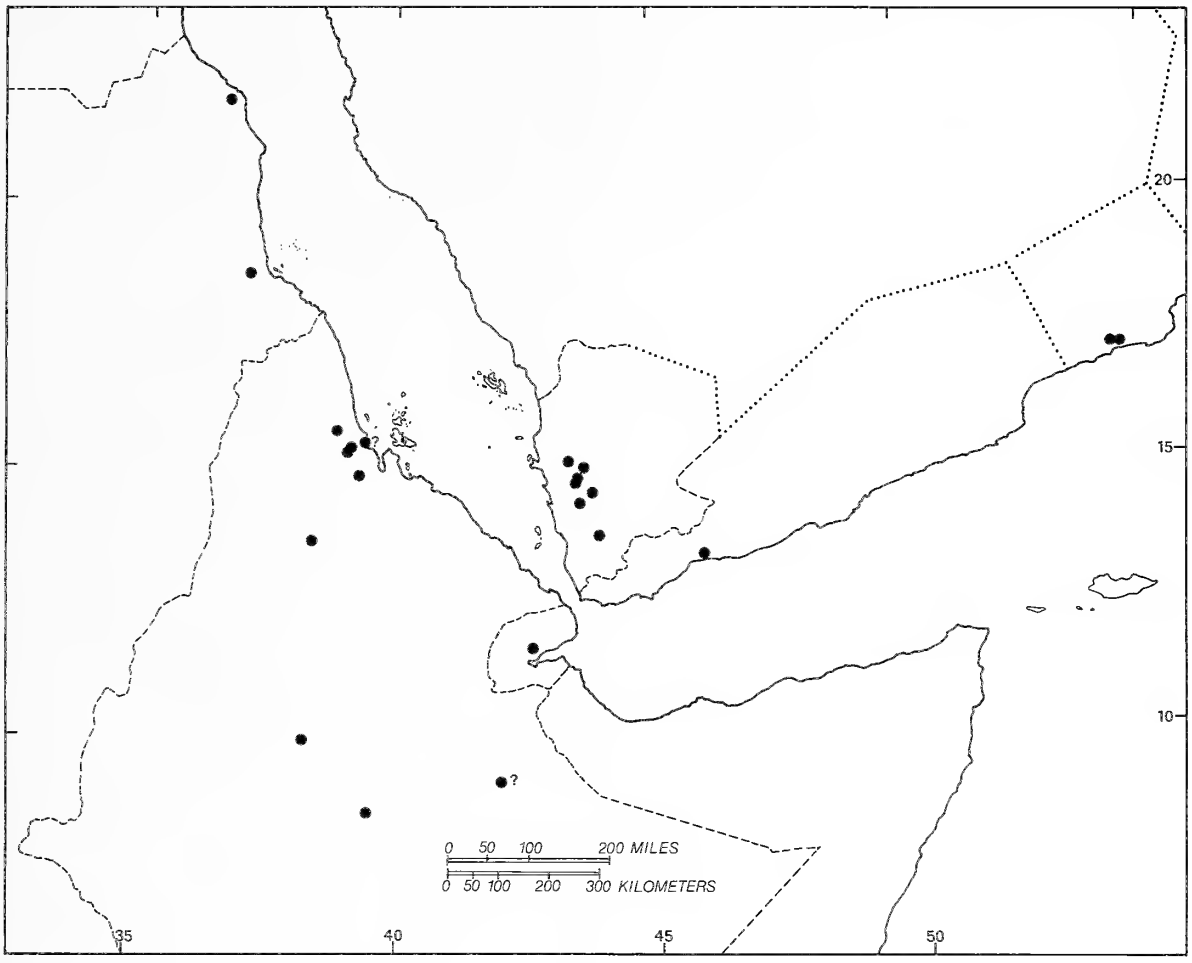
Inflorescences thyrses, terminal on the main shoots and frequently also on long or short axillary shoots, lax to moderately lax, ovoid to broadly ovoid, 2.5–6(–12.8) cm long, 2.5–6(–12) cm wide, with (1–)3–10(–12) cincinni, alternate or subopposite (rarely some subverticillate), ascending (occasionally the lower becoming patent or declinate). Peduncles 4–15(–22.5) cm long, puberulous. Inflorescence bract supramedial (rarely medial), herbaceous, bract-like or foliaceous. Inflorescence axis puberulous to subglabrous (rarely glabrous). Cincinni to 9.5 cm long and 21-flowered. Cincinnus bracts herbaceous to membranous, usually ascending and closely appressed to the cincinnus peduncles, ovate to ovate-elliptic or lanceolate-ovate (rarely narrowly lanceolate to lanceolate-elliptic), (1.2–)1.5–3(–5.5) mm long (the lowermost always longest and commonly perfoliate), prominently glandular subapically, also usually with smaller glands along the margin basally (marginal glands rarely absent), glabrous (rarely the lowermost sparsely puberulous). Cincinnus peduncles generally ± uniform within the inflorescence, exceeding the cincinnus bracts, (2.3–)4–12(–15.5) mm long, glabrous or sparsely puberulous. Cincinnus axes glabrous (rarely sparsely puberulous). Bracteoles attached (1–)3–7(–8.5) mm apart, herbaceous, ± symmetrically cup-shaped, perfoliate, (1.15–)1.3–2.2(–2.95) mm long, (0.5–)0.75–1.3(–1.75) mm high, prominently glandular subapically, with smaller glands along the margin, glabrous.

Flowers perfect and staminate, odorless, 11–18 mm wide (Plate 3*f*). Pedicels 4–8(–11.5) mm long in flower, to 12 mm long in fruit, ascending in flower, erect or recurved to ~150° in fruit, persistent, glabrous or very sparsely puberulous at the apex. Sepals prominently glandular near the apex, glabrous (very rarely with a few hairs at the base); medial sepal lanceolate-elliptic to ovate-elliptic, 2.1–4.2 mm long, ~1.7–2.3 mm wide, subapical gland bilobed (one sepal in *Deflers 968* also with a marginal gland); lateral sepals ovate-elliptic to oblong-elliptic (rarely suborbicular), 2.6–4.5 mm long, ~2 mm wide, subapical gland unlobed or bilobed. Paired petals white to pale shades of lilac, lavender, mauve or blue, limb ovate, apex ± obtuse, claw white or whitish, glabrous. Medial petal cup-shaped or slipper-shaped, 5.5–8(–10?) mm long, concolorous with paired petal limbs or paler than them. Lateral stamen filaments fused basally to medial stamen filament and to lateral staminode filaments (Figure 26*c*). Medial staminode with filament 1.5–1.8 mm long, antherode bilobed, lobes sessile, usually ± transversely elliptic, occasionally obovate-cuneate, connective elongate or not. Lateral staminodes with filaments 2–3.5 mm long, antherode bilobed, lobes sessile or subsessile, obovate-cuneate, 0.3–0.8 mm long, connective not elongate (rarely scarcely elongate). Lateral stamens with filaments 5.4–9.5 mm long, S-shaped, glabrous, anthers lanceolate-elliptic to elliptic or ovate-elliptic, 0.85–1.3(–2) mm long, pollen whitish, yellowish or golden yellow. Medial stamen with filament 4–6 mm long, anther ovate to ovate-elliptic (rarely lanceolate), saddle-shaped, 1.1–1.5(–2.5) mm long, pollen golden yellow, concolorous with lateral anther pollen or strongly discolorous. Ovary stipitate, obovate-subquadrate, 1.5–2(–3) mm long, densely covered with capitate, glandular hairs, apex emarginate, dorsal locule prominent (always?), 1-ovulate or empty, ventral locules (1–)2–3-ovulate; style (3–)6–9.5 mm long, arcuate-decurved, sometimes recurved towards the apex, sometimes curving out of the floral midplane, stigma capitate, held near or in contact with the lateral and/or medial anthers.

Capsules stipitate, obovate to obovate-oblong (rarely obovate-elliptic), dehiscent, bivalved, usually trilocular, (3.5–) 4.5–7.5(–8) mm long, (2.25–)3.3–4.5(–4.9) mm wide, buff to pale grayish tan or tan, frequently with small, scattered, brown spots, lustrous, glabrous or subglabrous, apex emarginate (rarely truncate), dorsal valve deciduous (rarely both valves deciduous in old capsules), dorsal locule prominent or not, when prominent, 1-seeded or, by abortion, empty, ventral locules each (1–)2–3-seeded, cells of the capsule wall transversely elongate or irregular. Dorsal locule seed convexo-planar, slightly humpbacked towards the capsule apex, elliptic to ovate-elliptic or oblong-elliptic, (2.4–)2.7–3.6 mm long, (1.5–)1.95–2.1 (–2.4) mm wide, 1.25–1.5 mm thick, hilum dark brown, in a shallow groove, shorter than the seed, testa buff-orange or buff, ± smooth, farinose granules and hypha-like filaments absent; ventral locule seeds (Plate 6*d*) ovate to triangular or trapezoidal, apical ventral seeds acute to obtuse or rounded apically, basal ventral seeds angular basally, (1.5–)1.8–2.6(–3.1) mm long, (1.4–)1.7–2.2(–2.5) mm wide, (1.1–)1.2–1.45(–1.55) mm thick, hilum blackish or dark brown, raised in a groove, usually slightly extended onto apical or basal surface, testa brown or gray-brown (occasionally buff-orange or orange-brown), shallowly scrobiculate or scrobiculate-reticulate (rarely shallowly foveolate), white or brownish farinose granules sparse in the depressions and around the embryotega, denser around the hilum, hypha-like filaments present among the farinose granules.

HABITAT.—Thickets, scrub, and dry forest, often near streams or seepage areas, commonly among rocks; partial or dense shade; (300–)600–1500(–1700?) m.

FLOWERING.—Flowering specimens have been seen from January–April, June, August–October, and December. From



MAP 13.—Distribution of *Aneilema forskalii* Kunth.

collection dates and condition of the specimens, July should be added. In cultivation the flowers are open in the morning, but exact opening and fading times have not been determined.

CHROMOSOME NUMBER.—$n = 26$, $2n = 52$.

DISTRIBUTION.—Red Sea Hills of Sudan, N and central Ethiopia, Djibouti, E Yemen Arab Republic, S Southern Yemen, and S Oman (Map 13).

SPECIMENS SEEN.—SUDAN. KASSALA: Erkowit (Jebel Seila), *Andrews A3589* (K); Erkowit, Red Sea Hill, *Aylmer 182* (K): Gebl Elba, Wadi Rabdit, *Drar 114* (S); Gebl Elba, *Drar 287* (S); Gebl Elba, Wadi Idaib, *Drar 300B* (S); Red Sea Hills, Hetatera, *Jackson 2804* (K); Red Sea Hills, below Erkowit, *Maffey 51* (K); Gebel Elba, Wady Ekwal, *Shabetai F1507 bis* (K); Gebel Elba, 23–27 Jan 1929, *Täckholm s.n.* (S).

ETHIOPIA. ERITREA: Ghinda, *Baldrati 933* (FT); Filfil-Marrao, *Baldrati 1387* (FT); Sul fiume Mederreba, Ghinda, *Baldrati 1388* (FT); Togodele, *Ehrenberg 413* (B, fragment L); Hamasen, Ghinda, *Fiori 874* (FT); Hamasen, Embatcalla, *Fiori 875* (FT); Amasen, Dongollo presso Ghinda, *Pappi 4511* (EA, G—2 sheets, MO, US); Au-dessous de Gheleb, *Schweinfurth 1416* (G—2 sheets); Gorge d'Ailet près Saati, *Schweinfurth & Riva 427* (G—2 sheets, K); Mont Bosco près Saati, *Schweinfurth & Riva 565* (G—2 sheets); Haïchello Kobob au nord d'Acrour, *Schweinfurth & Riva 1672* (G—2 sheets). HARAR: Rock valley 40 km from Harar, cultivated at Addis Ababa, *Mistry M-7* (EA). SHOA: Blue Nile Gorge, 3 km S of bridge on Addis Ababa–Debre Marcos [road], *Gilbert & Gilbert 2186* (K); Blue Nile Gorge, S side, *Gilbert & Thulin 969* (MO); ~40 km E of Nazareth, *de Wilde & de Wilde-Duyfjes 10529* (WAG). TIGRE: In valle fluvii Tacaze prope Dscheladscheranne [Djeladjeranne], *Schimper 1660* (B, G—2 sheets, K—2 sheets, M, MO, P—3 sheets, S; photo EA) and *1729* (G, K, P, S). TIGRE/BAGEMDER: Chiré, *Quartin Dillon 449* (P); without locality or date (ex Herb. de Franqueville & Herb. Cosson 18), *Quartin Dillon s.n.* (P); Bords du Tacazzé, *Quartin Dillon & Petit 449* (K) & *Quartin Dillon s.n.* (P–2 sheets; photo EA, K).

DJIBOUTI. District uncertain: Matoki, *Sabourеau 259* (P). TADJOURA: Goda Mts., steep gorge leading down to Wadi Toha, *Lavranos 11466* (K, MO).

YEMEN ARAB REPUBLIC. Without locality, 1837, *Botta*

s.n. (P); Montes Hadienses ad Bulgliose, *Forsskål in Herb. Forskalii 31* (C, photo US) and *32* and *33* (both C; photo K, MO); wadi above Suq Ar Ribat, Jebel Raymah, *Wood 1892* (F); between Suq Ar Ribat and Beni Danan on the Nagila path, Jebel Raymah, *Wood 1902* (F); Wadi Dur, Udayn, *Wood 1997* (F); above Suq As Sabt, Jebel Bura, *Wood 2173* (F); above the Wadi Yure between Jebels Hufash and Melhan, *Wood 2395* (F); above the Wadi Hijan, Usil in the Haraz, *Wood 2580* (F); N of Udayn Suq, *Wood 2895* (F); by the Wadi Sughna, Haimai al Dakhalia, *Wood 2959* (F); Gebel Bura, Hille, *Schweinfurth 289*, p.p. (G—2 sheets); Regma, Hodjela, *Schweinfurth 944*, p.p. (G—2 sheets).

SOUTHERN YEMEN. Bilad Fodhli, montis el'Areys, prope Serrya, *Deflers 968* (G—3 sheets, P).

OMAN. Arzat Road, 17°09′N, 54°14′E, *Mandaville 6860* (BM); Salalah–Thamarit road, 17°09′N, 54°08′E, *Mandaville 6886* (BM); Jariz Dhofar, foothills, *Vesey-FitzGerald 1236/8* (BM).

Discussion

The nomenclatural history of *A. forskalii* is one of the most complex in the genus. Forsskål's illegitimate name for the plants that he collected in the Yemen, *Commelina tuberosa*, was published posthumously (Forsskål, 1775). The basis for his specific name is unclear: the three specimens in the Forsskål Herbarium in Copenhagen lack bases, and Forsskål's description does not mention the roots. All collections of this species with bases and the living material observed in cultivation show only fibrous roots.

Vahl (1805–1806) appears to be the only botanist (with the possible exception of Schweinfurth) who studied Forsskål's collections of this species. He expanded Forsskål's description and changed the name to *Commelina paniculata*, which, unfortunately, was also illegitimate. Kunth (1843) properly placed this species in *Aneilema* and changed the specific epithet to honor the collector.

Richard (1850) described *Aneilema tacazzeanum* from two Ethiopian collections (*Quartin Dillon & Petit s.n.* and *Schimper 1660*). These collections clearly belong to one species, the only notable differences being the longer sepals and glabrous cincinnus axes in *Schimper 1660*. A comparison of these specimens with the syntypes of *A. forskalii* revealed no significant differences. Accordingly, *A. tacazzeanum* Hochstetter ex A. Richard has been placed in synonymy.

It should be noted that Richard (1850) omitted Petit's name as a collector, apparently inadvertently. The specimen from the Richard Herbarium, which is here chosen as the lectotype of *A. tacazzeanum*, has both Quartin Dillon's and Petit's names on the label. However, there is also a sheet in the Paris Herbarium with only Quartin Dillon's name on it, which is almost certainly part of the same collection, but it is not clear whether this specimen was seen by Richard. *Quartin Dillon 449* and *Quartin Dillon & Petit 449* are also part of the type collection.

The only previous worker to suggest that *A. tacazzeanum* is a synonym of *A. forskalii* was Schweinfurth (1894:59), who had collected plants on both sides of the Red Sea, including some from near the type locality of *A. forskalii*. Clarke, who had not seen Forsskål's collections, stated that such synonymy was highly unlikely and that, based on the description of Vahl (1805–1806) of *Commelina paniculata*, *A. forskalii* "was almost certainly a species of *Commelina*" (Clarke, 1901:66).

Richard's species has been much confused. Hasskarl (1864a) made the combination *Lamprodithyros tacazzeanus*, based on Richard's name, and he provided a very detailed description, but the latter was based on a collection from Mozambique (*Peters s.n.*), where the species does not occur. Brenan (1961) stated that the Mozambique collection was most likely *A. nyasense*, and a fragment that I found in the Leiden Herbarium (L), which came from Hasskarl's personal herbarium, has confirmed that. Similarly, *A. tacazzeanum* of Baker (1875) is *A. spekei;* that of Chiovenda (1939) is partly *A. somaliense* and partly *A. petersii* (not at all *A. tacazzeanum*); and that of Lewis (1964) is *A. recurvatum*.

Clarke (1881a) concluded that *Schimper 1660* was a mixed collection and that Richard (1850) had not selected the specimens that Hochstetter had intended to bear the name *Aneilema tacazzeanum*. Clarke (1881a) therefore distinguished *A. tacazzeanum* Hochstetter ex C.B. Clarke from *A. tacazzeanum* A. Richard, which he then described as *A. aequinoctiale* var. *minor*. Clarke's interpretation of Richard's *A. tacazzeanum* was based largely on the latter's description of the capsule locules being about six-seeded, which, as Brenan (1961) later pointed out, was evidently an error by Richard.

Clarke's distinction of *A. aequinoctiale* var. *minor* from *A. tacazzeanum* was challenged by Hua (1895:121), who noted that the plants annotated by Clarke as his var. *minor* were totally different from other collections of *A. aequinoctiale*. He further stated that the specimens of var. *minor* could not be distinguished from *A. tacazzeanum*. The response of Clarke to Hua's evidence was, "Hua appears to draw the line between the two species at a different point" (Clarke, 1901:66). Brenan (1961), however, examined the specimens upon which Richard (1850) based his *A. tacazzeanum*, including those used by Clarke for the description of *A. aequinoctiale* var. *minor*, and found them all conspecific and distinct from *A. aequinoctiale*. I fully concur with this conclusion. Both *A. aequinoctiale* var. *minor* and Clarke's *A. tacazzeanum* are therefore synonyms of *A. tacazzeanum* Hochstetter ex A. Richard.

Neither Hasskarl (1867) nor Schweinfurth (1894) mentions a collection number for the type of *Lamprodithyros ehrenbergii*, but *Ehrenberg 413* bears both Hasskarl's and Schweinfurth's handwriting on it, and it is clearly the type. The holotype consists of a sheet with two clearly annual plants mounted on it. The few small inflorescences lack flowers and have only two immature capsules. These plants differ from all other specimens of *A. forskalii* in having more densely pubcrulous cincinnus peduncles and axes, smaller bracteoles, and shorter

capsules. They also lack marginal glands on the cincinnus bracts, which are present in nearly all specimens of *A. forskalii*. Despite these differences, *Ehrenberg 413* agrees with *A. forskalii* in its annual habit, glabrous bracteoles with prominent marginal glands, more or less erect, moderately long fruiting pedicels that are puberulous only at the apex, and glabrous sepals. Even in the characters in which it departs from *A. forskalii*, *Ehrenberg 413* is connected to more typical specimens by a series of intermediates.

Although there is no direct evidence that *A. forskalii* can ever be a perennial, several particularly robust specimens make one wonder. *Schweinfurth 1416* and *Schweinfurth & Riva 1672* have particularly large bracteoles (2–2.75 mm long, 1–1.75 mm high) and frequent lateral inflorescence-shoots. They have the longest cincinnus bracts observed in the species, the bracts also being unusual in nearly always lacking marginal glands. Like these two collections, *De Wilde & De Wilde-Duyfjes 10529*, the southernmost collection of *A. forskalii*, has unusually long bracteoles and cincinnus bracts. These three collections otherwise agree with *A. forskalii*, and they probably represent no more than plants growing under very favorable conditions.

Mistry M-7 is known to me from a single specimen of a plant cultivated in Addis Ababa. On the basis of vegetative and inflorescence characters, it cannot be separated from *A. forskalii*. Its flowers, which have been very carefully pressed, appear to conform with specimens of this species except for the smaller size of some parts, e.g., medial petal 5.5 mm long and medial stamen filament 4 mm long. The style is particularly short, 3–4 mm long, and it is not recurved at the apex. The position of the stigma relative to the lateral anthers suggests self pollination. Whether the flowers of *Mistry M-7* are truly unusual for *A. forskalii* is difficult to ascertain, because so few specimens have measurable floral parts.

The most unusual characters of *Mistry M-7* are those of the capsules and seeds. The capsules are often obovate-elliptic, a shape rare in *A. forskalii*. Their width (2.25–3.25 mm) falls completely outside the range of other specimens of this species. The ventral locules are almost all one-seeded—a single two-seeded example has been noted—a character that, although known, is uncommon in *A. forskalii*. The ventral locule seeds are narrower and thinner than comparable seeds from other material of *A. forskalii*. Their elliptic shape and shallowly foveolate testa have not been found elsewhere in the species.

Mistry M-7 could readily be segregated from *A. forskalii* either at the specific or subspecific level on the basis of capsule and seed characters. I feel that such separation should await the availability of specimens pressed in the field in order to determine whether some of the peculiarities observed in *Mistry M-7* may have been due to cultivation conditions.

The pedicels of *A. forskalii* are less recurved than those of any other species of section *Lamprodithyros* with thyrsiform inflorescences except *A. sebitense*. They are sometimes erect, but more commonly the apex is recurved somewhat further. Great variation in fruiting pedicel length is found within inflorescences of some specimens, e.g., *Deflers 968*. Overall, variation in pedicel length is considerable in *A. forskalii*, but no clear geographic pattern is recognizable, although most specimens with particularly short pedicels are from Eritrea (but so are some very longly pedicellate ones!).

Petal color, rarely noted by collectors, appears to be white or paler shades of bluish or pinkish purple. The possible yellow color, described by Andrews (1956) for Sudanese plants and perhaps based only on the collector's notes on *Aylmer 182*, is most likely erroneous.

Staminodes have been seen in many flowers and buds. The differentiation between the medial and lateral antherodes—lobes wider than long in the medial antherode and longer than wide in the lateral antherodes—is probably constant in this species. The antherodes are all yellow.

The number of seeds per ventral locule varies from one to three. No collection definitely has solely one-seeded nor solely three-seeded ventral locules, although several show only two-seeded ventral locules. The one-seeded locules do not appear to be the result of abortion of ovules in many cases, but rather to the presence of solitary ovules in the ovary. Similarly, the absence of a dorsal locule seed in the capsules of *Gilbert 3941* was probably due to the absence of an ovule in that locule of the ovary (noted in the one ovary which could be dissected), not to abortion.

A decrease in the number of seeds per ventral locule within the inflorescence has been noted in *Deflers 968*. The first capsules produced within the inflorescences are the largest and have two-seeded ventral locules. They also have the longest pedicels. Later capsules are smaller and have only one-seeded locules. Similar variation has not been noted in other collections.

An altitude of 1700 m is recorded on both sheets of *Schweinfurth 1416;* however, the same collection is listed as 1500 m by Schweinfurth (1894). Several collections made by Wood are also from about 1500 m, and that is the highest confirmed altitude for *A. forskalii*.

The records of *A. forskalii* (as *A. tacazzeanum*) from Egypt (Täckholm and Drar, 1950) appear to be based on old boundaries between that country and Sudan. All of the specimens are from the Gebel Elba area, which is shown in modern maps to be part of Sudan. *Aneilema forskalii* should be expected to occur in the mountains of northern Somali Republic (Lavranos, personal communication), but it has not yet been collected in that country.

In addition to the specimens seen for this study, further collections are cited by Schweinfurth (1894) and Täckholm and Drar (1950). It is uncertain whether any of the Schweinfurth collections cited by him but not seen by the writer still exist. None are in the Berlin Herbarium.

Despite great variation, *Aneilema forskalii* is a very distinctive species because of its annual habit, small cincinnus bracts with generally glandular margins, usually glabrous or

subglabrous cincinni, relatively thick-textured, widely spaced, nearly symmetric bracteoles with conspicuous marginal glands, generally erect or only slightly further recurved, glabrous or subglabrous fruiting pedicels, glabrous sepals, and large, longly stipitate, glabrous, humpbacked capsules sometimes with three seeds in each ventral locule. *Aneilema forskalii* appears to be most closely related to *A. recurvatum, A. sebitense,* and *A. woodii*. From the first species it differs by its generally glandular cincinnus bract margins, more widely spaced bracteoles, generally more erect fruiting pedicels, paler flowers, larger, more longly stipitate, ± glabrous capsules, and larger seeds. For differences from *A. sebitense* and *A. woodii*, see the key and discussions under those species.

6. *Aneilema woodii* Faden, new species

Herbae perennes foliis plerumque spiraliter dispositis, laminis lanceolatis ad lanceolato-ellipticas, lanceolato-ovatas vel ovato-ellipticas, 5–10(–13) cm longis, (1.5–)2–4.5 cm latis, supra pilis longis uniseriatis plerumque carentibus. Inflorescentiae thyrsi ovoidei, ad 5 cm longas et 7 cm latas, cincinnis 2–9 compositi. Bracteolae 0.8–3 mm semotae, membranaceae, cupulatae (symmetrice vel asymmetrice), plerumque perfoliatae, 1.5–2 mm longae, ad 1 mm altas, puberulae, glandibus marginalibus carentibus. Pedicelli 4.5–7.5 mm longi, tempore fructigero recurvati plerumque ~180°, puberuli. Sepala purberula. Capsulae stipitatae, dehiscentes, triloculares, 5–7 mm longae, 4–5 mm latae, loculo dorsali plerumque 1-seminali, loculis ventralibus uterque plerumque 2-seminalibus. Semen loculi dorsalis 2.7–3.2 mm longum, 2.1–2.5 mm latum, 1.4–1.8 mm crassum, testa laevi. Semina loculorum ventralium 1.9–2.9 mm longa, 1.9–2.4 mm lata, testis reticulato-foveolatis non profunde (Figure 51).

TYPE.—Yemen [Yemen Arab Republic; Yemen (Sana'a)], just above Hilla, Jebel Bura, 15 Feb 1980, *Wood 2616B* (living only); pressed from cultivation 4 Nov 1980 and other dates (US, holotype; EA, F, K, MO, P, isotypes).

Perennial herb (habit types IB, IC, Figure 1). Roots fibrous. Shoots erect to ascending (sometimes decumbent?), to more than 1 m tall in cultivation. Internodes (2–)5–7(–15) cm long, green, puberulous at least below the nodes. Leaves spirally arranged (rarely distichous in part), sheaths 1–2.5 cm long, puberulous, also sparsely pilose (particularly at their bases), ciliate at the apex, laminae petiolate, lanceolate to lanceolate-elliptic, lanceolate-ovate or ovate-elliptic, 5–10(–13) cm long, (1.5–)2–4.5 cm wide, apex acuminate, margin undulate, scabrid, sparsely ciliate basally, adaxial surface puberulous, typically lacking long, uniseriate hairs, pale-veined, abaxial surface pilose-puberulous.

Inflorescences thyrses (Figure 51*b*), terminal on the main flowering shoots and on axillary inflorescence-shoots from the inflorescence bract and upper leaves (the lowermost of these inflorescence-shoots perforating the subtending leaf sheath, Figure 51*a*), moderately lax, ovoid, to 5 cm long and 7 cm wide, with 2–9 cincinni, alternate to subopposite, ascending to (in the lowermost cincinni) patent. Peduncles 3–12 cm long, puberulous. Inflorescence bract usually supramedial, bract-like or foliaceous. Inflorescence axis puberulous. Cincinni to 3.5(–5.5) cm long and 15(–17)-flowered. Cincinnus bracts membranous, appressed to the cincinnus peduncles or patent, lanceolate-oblong to ovate, 1.5–4(–6) mm long, glandular subapically (apparent only in young inflorescences), puberulous. Cincinnus peduncles relatively uniform within the inflorescence, exceeding the cincinnus bracts, 4–9(–11) mm long, puberulous. Cincinnus axes puberulous. Bracteoles attached 0.8–3 mm apart, membranous, cup-shaped (symmetrically or asymmetrically), usually perfoliate, 1.5–2 mm long, to 1 mm high, glandular subapically but not along the margins, puberulous.

Flowers perfect and staminate, odorless, 10.5–17 mm wide (Figure 51*c,d;* Plate 3*g*). Pedicels 4.5–6 mm long in flower, to 7.5 mm long in fruit, ascending in flower, recurved generally ~180° in fruit (Figure 51*i*), persistent, puberulous in the apical 1/2–3/4. Sepals glandular subapically with unlobed glands, puberulous; medial sepal elliptic to ovate-elliptic, 3–4.5 mm long, ~3 mm wide, subapical gland prominent; lateral sepals not reflexed, broadly elliptic to obovate-elliptic, 4–5 mm long, 3.5–4 mm wide, subapical gland not prominent. Paired petals 8–11 mm long, 8–10 mm wide, limb broadly ovate to ovate-reniform, 6–8 mm long, white faintly tinged with pink, apex rounded; claw concolorous, 2–3 mm long, glabrous. Medial petal cup-shaped, obovate to broadly elliptic-obovate (Figure 51*c,d*), broadest at the margin (viewed from the petal apex), apparently not retaining the lateral stamens when the flower opens, 7–8 mm long, 5–6.5 mm wide, 3.5–4.5 mm deep, concolorous with paired petals. Stamen filament bases shortly fused, staminodes ± free (Figure 51*g*). Medial staminode with filament ~3–3.5 mm long, white shading to yellow at the apex, antherode bilobed, yellow, lobes ± sessile, curving downward, ± obliquely transversely elliptic, ~0.7 mm long, connective not or scarcely elongate (Figure 51*e*). Lateral staminodes with filaments ~5.5–6.5 mm long, white shading to yellow apically, antherodes bilobed, ± bowtie-shaped, yellow, lobes ± sessile, obovate, ~0.9 mm long, connective not elongate (Figure 51*f*). Lateral stamens with filaments ± parallel and held close together, S-shaped, 9–10.5 mm long, glabrous, anthers elliptic to ovate-elliptic, ~1 mm long, pollen golden yellow. Medial stamen with filament ~7 mm long, anther ovate to ovate-elliptic, saddle-shaped, ~1.5 mm long, pollen ± concolorous with lateral anther pollen. Ovary stipitate (Figure 51*h*), obovate, ~2 mm long × 1.5–1.8 mm wide, densely and ± uniformly covered with patent (but apically pointing) glandular hairs, apex truncate, dorsal locule prominent, 1-ovulate, ventral locules 2-ovulate; style 8–8.5 mm long, arcuate-decurved after the ovary, slightly recurved near the apex, also strongly curved out of the floral midplane, stigma slightly capitate, held at the same level as the lateral anthers and frequently making contact with them.

Capsules stipitate (Figure 51*i*), obovate to obovate-elliptic,

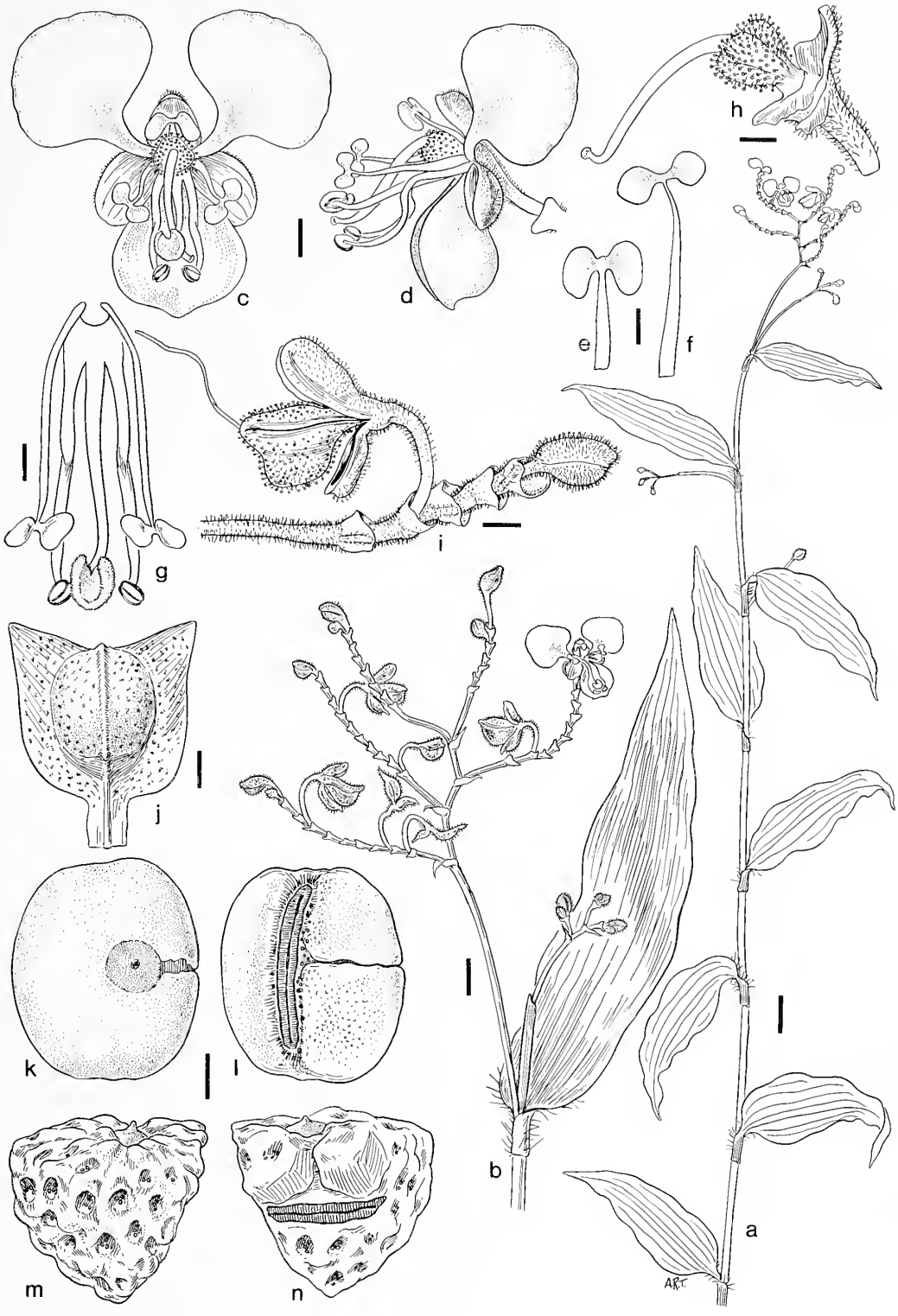


FIGURE 51.—*Aneilema woodii* Faden, new species: *a*, flowering shoot; *b*, inflorescence; *c*, perfect flower, front view; *d*, perfect flower, side view; *e*, medial staminode; *f*, lateral staminode; *g*, androecium, top view, medial staminode omitted, gynoecium removed; *h*, gynoecium, side view; *i*, capsule attached to cincinnus, side view; *j*, dorsal capsule valve, dorsal view; *k*, dorsal locule seed, dorsal view; *l*, dorsal locule seed, ventral view; *m*, ventral locule seed, dorsal view; *n*, ventral locule seed, ventral view (all from *Wood 2616B*). (Bars = 20 mm for *a*; 5 mm for *b*; 2 mm for *c,d,i*; 1 mm for *e-h,j*; 0.5 for *k-n*.)

dehiscent, bivalved, trilocular, 5–7 mm long, 4–5 mm wide, carinate middorsally, stramineus to gray-brown, flecked with dark brown, lustrous, puberulous, apex emarginate, dorsal valve deciduous, dorsal locule very prominent, humpbacked (Figure 51*j*), 1-seeded or, by abortion, empty, ventral locules each 2-(or, by abortion, 1-)seeded, cells of the capsule wall mainly transversely elongate, occasionally isodiametric to longitudinally elongate. Dorsal locule seed (Figure 51*k,l*) slightly humpbacked towards the capsule apex, broadly oblong-elliptic, 2.7–3.2 mm long, 2.1–2.5 mm wide, 1.4–1.8 mm thick, hilum dark brown, in a shallow groove, shorter than the seed, testa buff, smooth, lacking farinose granules and hypha-like filaments. Ventral locule seeds (Figure 51*m,n*) ovate to deltate or trapezoidal, apical seed thickened and ± obtuse apically, basal seed somewhat angular basally, 1.9–2.9 mm long, 1.9–2.4 mm wide, 1.2–1.8 mm thick, hilum dark brown, raised in a groove, slightly extended onto apical and basal surfaces, testa buff, shallowly reticulate-foveolate, with dark brown or grayish farinose granules sparse in the depressions and around the embryotega, denser around the hilum, with hypha-like filaments sparse among the farinose granules around the hilum.

HABITAT.—Scrub, track sides, rocky slopes and cliffs in rainfall areas of ~400–1000 mm per annum (Wood, in litt.); ~600 m.

FLOWERING.—Wood (in litt.) reports the plant flowering in mid February, "the driest time of the year." Because he collected mature capsules and seeds, the plants must also have been flowering in January.

CHROMOSOME NUMBER.—$n = 26$.

DISTRIBUTION.—Rare, local endemic in the Yemen Arab Republic (Map 14).

SPECIMENS SEEN.—YEMEN ARAB REPUBLIC. Jebel Bura, Hille [= Hilla], *Schweinfurth 289*, p.p. (G) (mixture with *A. forskalii*); Regma, Hodjela [= Hojeilah], *Schweinfurth 944*, p.p. (G) (mixture with *A. forskalii*); Jebel Bura, just above Hilla, *Wood 2616B* (EA, F, K, MO, P, US).

DISCUSSION

This species is named for J.R.I. Wood, whose invaluable recent collections and notes have enabled me to establish the identity of the nineteenth-century gatherings made by Schweinfurth.

Aneilema woodii differs from *A. forskalii*, its closest relative, in its perennial habit, general absence of long, uniseriate hairs from the adaxial leaf surface, more densely puberulous cincinnus peduncles and axes, more shortly spaced, thinner textured, pubescent bracteoles that lack marginal glands, shorter, more pubescent pedicels that are generally more recurved in fruit, puberulous sepals, broader medial petal, larger, more circular antherode lobes, concolorous pollen in all three anthers, and thicker, proportionally broader dorsal locule seeds.

My suggestion (Faden, 1975:251) that Schweinfurth's plants, then the sole collections of this taxon, might be closely related to *A. petersii* (despite the noted disjunct distributions) has proven to be unfounded. From that species, *A. woodii* differs most conspicuously in the general absence of long, uniseriate hairs from the adaxial leaf surface, more symmetric and generally perfoliate bracteoles that lack long, uniseriate hairs, differently shaped petals, and parallel lateral stamen filaments. In addition, *A. woodii* is tetraploid, whereas *A. petersii* is consistently diploid.

The recognition of *A. woodii* as a distinct species was prevented initially by the incomplete condition of the then available material. This problem was compounded by Wood's collections 2126, 2128, and 2616A, which at first I considered conspecific with Schweinfurth's collections (which were themselves parts of mixed collections with *A. forskalii*), despite their intermediate morphology between Schweinfurth's plants and typical *A. forskalii*. The living plant grown from a fleshy base of the specimen *Wood 2616A* failed to produce capsules in spite of repeated, induced self-pollinations, and thus a description of this taxon could not be finished.

This problem was finally resolved when Mr. Wood collected yet another living plant for me (as well as dried infructescences, capsules, and seeds) in February 1980 (*Wood 2616B*). This second plant produced flowers that differed in some details from those of *Wood 2616A*, e.g., considerably longer stamens, but, more significantly, it much better matched the original Schweinfurth specimens than did Wood's first three collections. The new plant was self-compatible and autogamous, and thus it soon produced capsules and seeds, enabling me to complete the description. The problem remaining was the interpretation of Wood's earlier collections (see below).

Aneilema woodii appears to be genuinely rare rather than just inadequately collected. Wood (in litt.) states that although he had an eye open for the plant for two years he found it at only one locality.

6a. *Aneilema woodii* × *forskalii*

PLATE 3*g*

HABITAT.—In scrubby vegetation; ~500–700 m.

FLOWERING.—November.

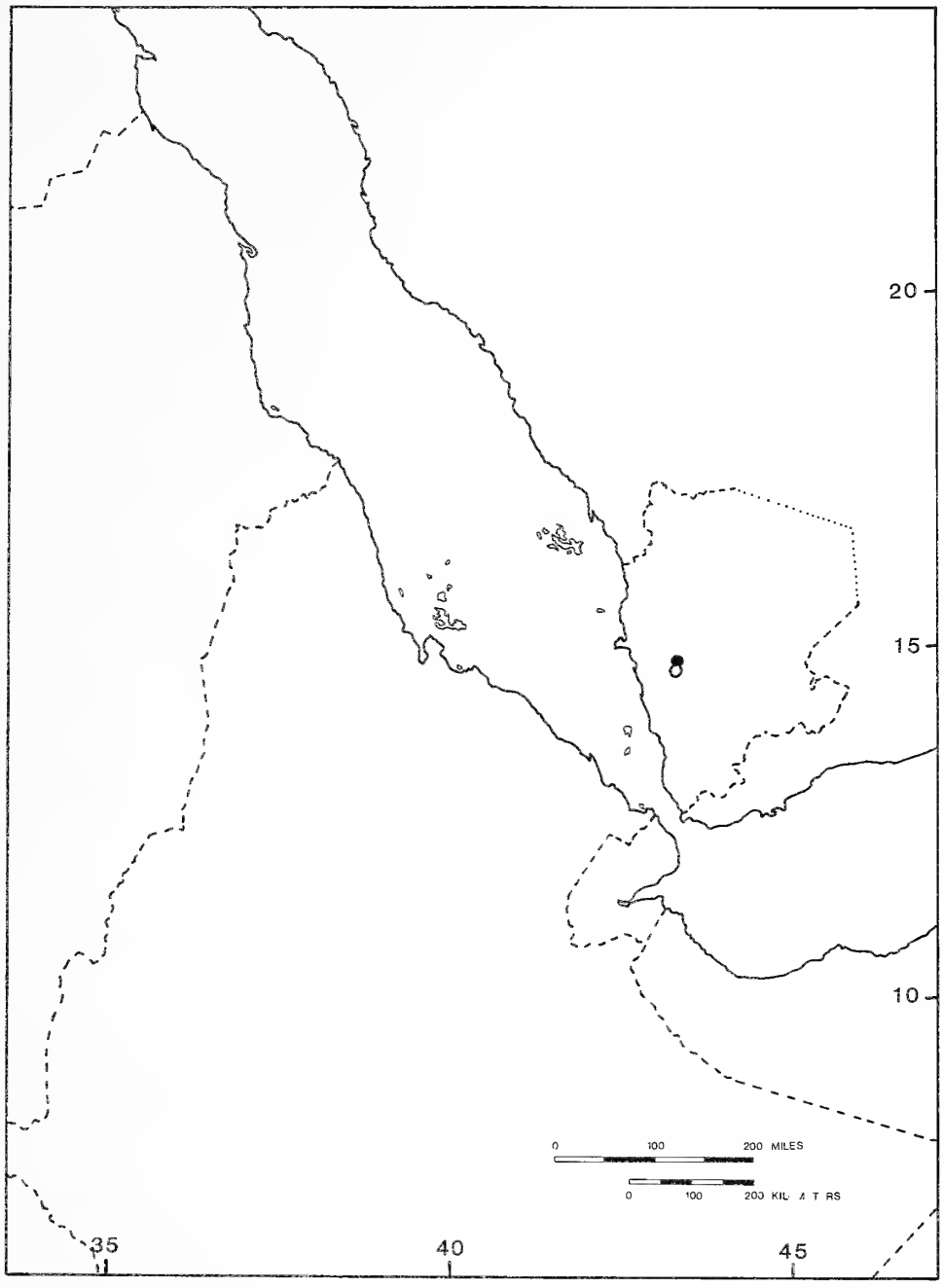
CHROMOSOME NUMBER.—$2n = 52$.

DISTRIBUTION.—The Yemen Arab Republic (Jebel Bura) (Map 14).

SPECIMENS SEEN.—YEMEN ARAB REPUBLIC. Jebel Bura, head of Wadi Hille [= Hilla], *Wood 2126* (F); Jebel Bura, just above the suq, Hille, *Wood 2128* (F); Jebel Bura, just above Hilla, *Wood 2616A* (F).

DISCUSSION

The above cited specimens are morphologically intermediate between *A. woodii* and *A. forskalii*. The living plant of *Wood 2616A* is apparently sterile. Its buds frequently fail to open, and



MAP 14.—Distribution of *Aneilema woodii* Faden, new species (solid and open dots), and *A. woodii* × *forskalii* (open dot).

self-pollination never leads to fruit set. The pollen was found to be 100% abortive, based on their mostly shrunken appearance and poor staining with cotton blue (in marked contrast to the pollen of *A. woodii*). The absence of fruits on the field collected specimens of all three collections, despite the presence of large inflorescences on *Wood 2128* and *2616A* (a combination of characters that is unusual in *Aneilema* section *Lamprodithyros*), further suggests that these plants are sterile hybrids.

The hybrids may be distinguished from *A. woodii* by the presence of long, uniseriate hairs on the adaxial leaf surface, generally more widely spaced (up to 5 mm apart), glabrous (or with a few hairs basally) bracteoles that have some marginal glands, and less pubescent pedicels (hairy in the apical $^1/_4$–$^1/_3$ of their length) and sepals. From *A. forskalii* they differ in their perennial habit and more densely pubescent cincinnus peduncles, cincinnus axes, pedicels and sepals.

The hybrids may be of relatively recent origin, for Schweinfurth collected only pure *A. woodii* and *A. forskalii*. Wood (in litt.) states that although the two species are identical in their ecology they do not occur together. On Jebel Bura *Aneilema woodii* and the hybrids are restricted to the valley above Hilla. *Aneilema forskalii* is apparently absent from that valley, but it occurs in the adjacent valley above Suq As Sabt (Wood, in litt.). Hybridization may have occurred as a result of moderately long distance pollen transfer by an insect vector. Alternatively, the annual *A. forskalii* may formerly have occurred in the same valley as *A. woodii* and may have died out there, leaving behind *A. woodii* and the perennial hybrids.

Some reproductive isolation between *A. woodii* and *A. forskalii* may occur as a result of partially discrete flowering seasons. *Wood 2616B* was collected in February, during the dry season, when *A. forskalii* would not be expected to be in flower (unless there were unseasonal rains) (Wood, in litt.). However, at the height of the rains, both species should be expected to be flowering concurrently, which the presence of hybrids ipso facto demonstrates.

7. *Aneilema benadirense* Chiovenda

Aneilema benadirense Chiovenda ["Benadirensis"], Atti Ist. Bot. Univ. Pavia, ser. 4, 7:154, pl. 12, 1936.—Cufodontis, Bull. Jard. Bot. Natl. Belgique, 41, suppl., 1517, 1971. [Type: Somali Republic, Basso Uebi Scebeli, sud di Merca, 15 Oct 1934, *Ciferri 73* (PAV, holotype; FT, K, isotypes) (Figure 52).]

Herbs, probably perennial (habit type unknown). Roots unknown. Flowering shoots apparently erect to ascending, to 22 cm long (including the inflorescence) in the specimens. Internodes 2–5 cm long, densely puberulous in longitudinal bands below the fused edges of the sheaths, otherwise sparsely puberulous to glabrous. Leaves spirally arranged, sometimes gradually reduced in size towards the apices of the flowering shoots, sheaths (5–)7–15 mm long, pilose-puberulous, ciliate at the apex, laminae sessile or occasionally very shortly petiolate, narrowly lanceolate-elliptic to lanceolate or ovate-lanceolate, 3.5–8 cm long, 1.5–2.3 cm wide, apex acuminate to acute, margin planar or slightly undulate, scabrid, sparsely ciliate towards the base and on the petiole (when present), upper leaves ciliate to a greater extent than the lower, adaxial surface pilose-puberulous, abaxial surface puberulous.

Inflorescences thyrses, terminal and occasionally axillary from the inflorescence bract and uppermost leaves, moderately dense, ovoid to ovoid-ellipsoid, (2.5–)3–5.5 cm long, 2–4 (–5.5) cm wide, with 10–21 cincinni (axillary inflorescences with perhaps fewer), alternate, subopposite or, commonly, subverticillate, ascending to patent (the lower becoming declinate with age). Peduncles 2–4 cm long, puberulous. Inflorescence bract usually supramedial (rarely submedial, subapical or, apical), herbaceous and foliaceous (or rarely, membranous and very reduced). Inflorescence axis puberulous. Cincinni to 2.5 cm long and 5-flowered. Cincinnus bracts membranous (rarely the lowermost herbaceous and ± foliaceous), appressed to the cincinnus peduncles or patent, ovate to ovate-elliptic, 1.5–2(–2.3) mm long, usually glandular near the apex, glabrous. Cincinnus peduncles relatively uniform within the inflorescence, exceeding the cincinnus bracts, (3–)4–7(–8) mm long, puberulous. Cincinnus axes puberulous. Bracteoles attached (1.5–)2–3(–3.3) mm apart, ± herbaceous, slightly eccentrically to nearly symmetrically cup-shaped, perfoliate, 1.5–1.7 mm long, 0.9–1.2 mm high, with a very prominent subapical gland and smaller glands along the margin, glabrous except for a few hook-hairs occasionally present at the base.

Flowers perfect and staminate. Pedicels (5–)6–7.5(–9) mm long, ascending and straight or arcuate in flower, in fruit, recurved (uniformly or predominantly above the middle) 180°–270°, persistent, glabrous below the middle, puberulous above. Sepals prominently glandular near the apex, with smaller glands along the margins; medial sepal apparently lanceolate or lanceolate-elliptic, 2.6–3.5(–4.3) mm long, glabrous, subapical gland deeply bilobed; lateral sepals apparently ± elliptic, 2.7–4(–4.5) mm long, glabrous or with a few hook-hairs towards the base, subapical gland unlobed or slightly bilobed. Paired petals ~6–8 mm long, limb 4.5–6.5 mm long, to 6 mm wide (Chiovenda, 1936); claw 1–1.5 mm long. Medial petal apparently slipper-shaped, 4.5–6(–7) mm long, ~2–2.5 mm deep. Lateral stamen filaments fused basally to medial stamen filament and to the lateral staminode filaments, medial staminode free. Medial staminode vestigial (always?), represented by a filament less than 1 mm long, antherode not developed. Lateral staminodes with filaments 2.5–3 mm long, yellow apically, antherodes bilobed, yellow, lobes shortly stipitate, obovate-cuneate to transversely elliptic, 0.6–0.8 mm long, connective not elongate. Lateral stamens with filaments 6–7 mm long, ± S-shaped, anthers lanceolate-elliptic, (0.9–)1–1.2(–1.4) mm long, ~0.5 mm wide. Medial stamen with filament 3.5–4(–4.3) mm long, anther ovate-oblong, saddle-shaped, 1.3–1.8 mm long, 0.8–1.2 mm wide. Ovary substipitate, ~1 mm long, densely covered with minute glandular hairs (hook-hairs apparently absent), dorsal locule very prominent, 1-ovulate, ventral locules each 2-ovulate; style 7–8 mm long, stigma slightly capitate.

Capsules substipitate, probably obovate-elliptic to obovate, dehiscent, bivalved, trilocular, 3.4–4 mm long, ~2 mm wide, grayish tan with dark brown spots on the dorsal locule, lustrous, sparsely puberulous, apex emarginate, dorsal valve deciduous (tardily?), dorsal locule very prominent, 1-seeded, ventral locules each 2-(or, by abortion, 1-)seeded, cells of the capsule wall transversely elongate. Dorsal locule seed (Plate 6*e*) hemispherical, 1.8–2 mm long, 1.3–1.4 mm wide, 1–1.25 mm thick, hilum dark brown, arising from a shallow groove in the flat, ventral surface, much shorter than the seed, testa yellowish buff or orange-buff, ± smooth, lacking white-farinose granules and hypha-like filaments except around the hilum where both are abundant. Ventral locule seeds (Plate 6*e*) ovate to subtriangular, apical seed rounded apically, basal seed angular

FIGURE 52.—Holotype of *Aneilema benadirense* Chiovenda (*Ciferri 73*—PAV).

basally, 1.3–1.6(–1.7) mm long, 1.35–1.4 mm wide, 0.9–1 mm thick, hilum dark brown, raised within a groove, not extended onto apical and basal surfaces, testa orange-buff, shallowly scrobiculate on all surfaces, sparsely white-farinose in most of the depressions, densely so around the hilum and embryotega, hypha-like filaments common among the farinose granules.

HABITAT.—Dunes and littoral (*Ciferri 73*), probably just above sea level.

FLOWERING.—The single collection is from October and has flowering and fruiting specimens. Unless the capsules and seeds mature unusually rapidly in this species, the largest inflorescences must have been flowering in September.

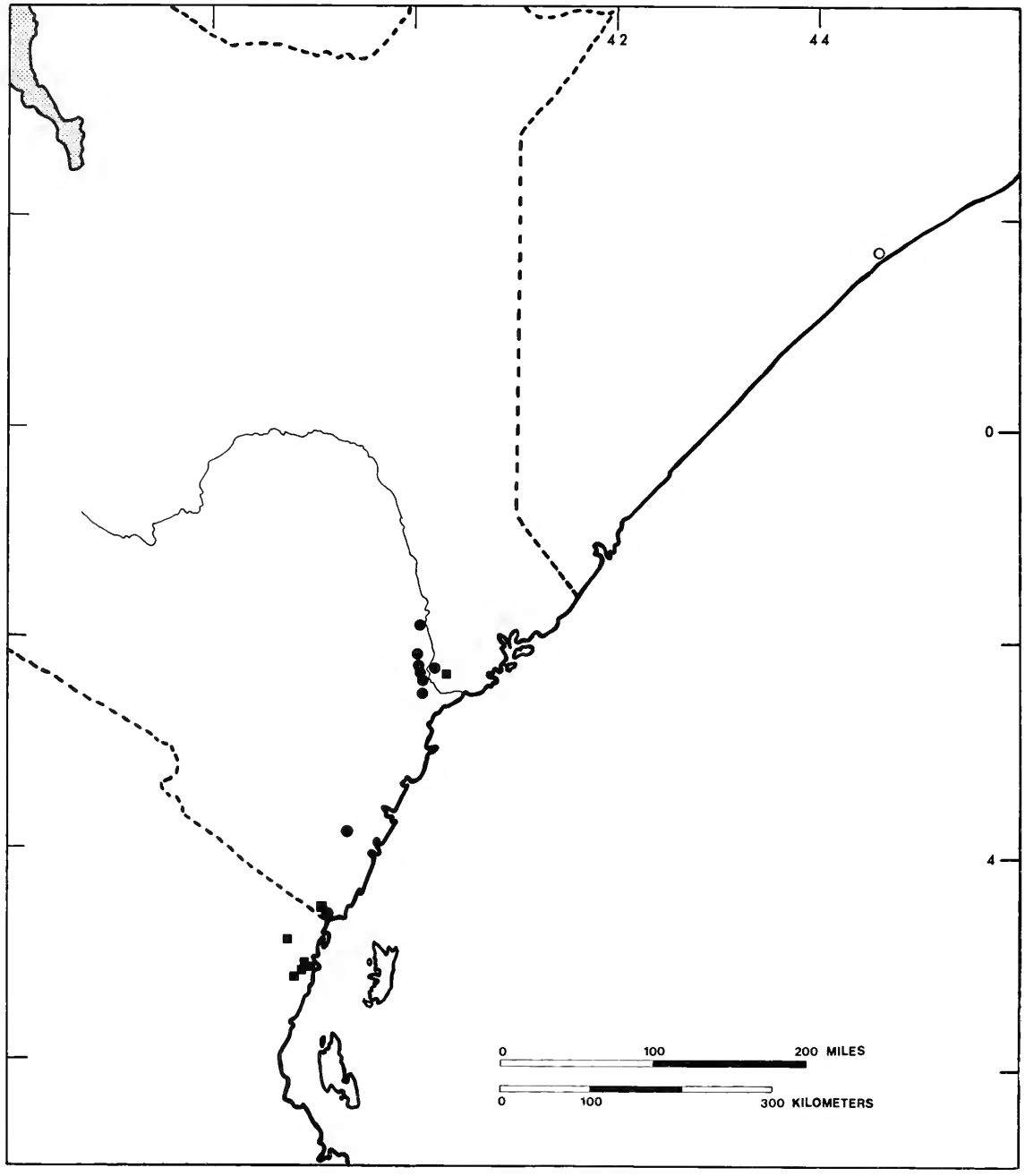
CHROMOSOME NUMBER.—Unknown.

DISTRIBUTION.—S Somali Republic (Map 15).

SPECIMENS SEEN.—SOMALI REPUBLIC. BENADIR: Basso Uebi Scebeli [River], sud di Merca, *Ciferri 73* (FT, K, PAV).

DISCUSSION

The holotype consists of the ten shoots illustrated in the plate accompanying the type description. They are, however, somewhat differently arranged than in the figure (Figure 52). All of the shoots lack bases and none has roots.



MAP 15.—Distribution of *Aneilema benadirense* Chiovenda (open circle), *A. calceolus* Brenan (solid squares), and *A. tanaense* Faden (solid circles).

The measurements given above frequently differ from those of Chiovenda (1936). In most cases the discrepancies are minor; in several they are significant and appear to be the result of Chiovenda's either not having noted the full range of variation shown in the material (distance between bracteoles, sepal length) or perhaps not having measured the best pressed flowers (lateral staminode filament length). For several characters (cincinnus peduncle length, medial anther length and width, dorsal locule seed length and width) Chiovenda's dimensions are quite wrong and should be ignored.

Nearly all of the shoots of the specimens have their longest leaves at the base, suggesting that even longer leaves may have been present on the lower, uncollected portions. Such leaves could well have been longly petiolate, for regularly petiolate lower leaves and sessile or subsessile upper leaves are common in other *Aneilema* species.

In the larger inflorescences of the specimens, usually all of the cincinni are subverticillate (or a few subopposite). In the smaller ones, however, the arrangement of the cincinni is less regular, generally some of them being alternate.

The abaxial leaf surfaces, inflorescence axes, cincinnus peduncles and axes, and occasionally the pedicels all appear to be covered with a mixture of hook-hairs and patent, glandular hairs of similar size. The swollen tips of approximately 15 of the seemingly glandular hairs were gently rubbed with a moistened camel's-hair brush and found to really be hook-hairs in which the terminal hook had become covered with adherent foreign matter, giving it the appearance of a clavate gland. It is likely that all of the apparent gland-tipped hairs on the above structures can be accounted for in this manner.

Some of Chiovenda's interpretations of floral characters are inaccurate. His description of the flowers as sometimes having two large-anthered stamens, in addition to the two smaller-anthered ones, was evidently based on two flowers pressed one upon the other (visible under a dissecting microscope in the top, right hand shoot in Chiovenda (1936, pl. 12) and Figure 52. Only one such anther is ever present. Chiovenda's designation of the stamens as five to six is likewise based on this erroneous observation of the medial stamen. The three stamens and lateral staminodes (his "five stamens") are always well developed. The medial staminode, apparently always vestigial, seemingly was overlooked by Chiovenda. The flower color, "greenish-white or yellowish-white," as cited from the collector by Chiovenda, is almost certainly incorrect.

Several important characters cannot be determined with certainty from the specimens. The rather long lateral stamen filaments and their apparent strong curvature suggest a well-developed stamen-retention mechanism. The dorsal capsule valve appears to become detached at the base even before the capsules are fully mature. While this is certainly an artifact of specimen preparation, it may indicate that this valve is normally deciduous in mature capsules.

The floral and capsular structure of *A. benadirense* clearly demonstrate that it belongs to section *Lamprodithyros*. Within the section, its regularly thyrsiform inflorescences suggest affinities with *A. forskalii, A. sebitense, A. recurvatum, A. petersii, A. indehiscens,* and *A. woodii.* It differs from *A. forskalii* and *A. sebitense* in its less widely spaced bracteoles and much smaller capsules and seeds, from *A. recurvatum* in its more strongly dimorphic seeds, and from all three in its more recurved fruiting pedicels. It can be separated from *A. petersii* and *A. indehiscens* by its more symmetric bracteoles, from *A. woodii* by its smaller seeds, and from all three by its glabrous or subglabrous bracteoles with marginal glands, glabrous or subglabrous sepals and smaller capsules. It further differs from all six of these species in its generally more numerous cincinni per inflorescence, usually glandular medial sepal margins (rarely present in *A. recurvatum* and *A. forskalii*) and vestigial medial staminode.

The closest relationship of *A. benadirense* is with *A. tanaense*. Both species have cincinni predominantly whorled, bracteoles and sepals with marginal glands, fruiting pedicels often recurved more than 180°, capsules with deciduous or possibly deciduous dorsal valves, and seeds strongly dimorphic. The general absence or rare vestigial presence of a medial staminode in *A. tanaense* also suggests an affinity with *A. benadirense*. The latter may be distinguished from *A. tanaense* by its generally longer leaves, larger, always thyrsiform inflorescences with more numerous cincinni, longer cincinnus peduncles, more widely spaced bracteoles, glabrous or subglabrous sepals, lack of hook-hairs on the ovaries and capsules, and larger capsules.

The single collection of *Aneilema benadirense* and a recent gathering of *A. petersii* subsp. *pallidiflorum* are the sole collections of section *Lamprodithyros* from the Somali Republic. In view of the diversity of taxa in this section recorded from the Kenya coast south of Lamu, further exploration in the poorly collected region north of that town and in the coastal areas of southern Somali Republic may well yield additional taxa.

8. *Aneilema tanaense* Faden

Aneilema tanaense Faden, Bothalia, 15:98, 1984. [Type: Kenya, Tana River District, Garissa–Malindi road, 16 km N of junction for Garsen, –2°08′S, 40°04′E, 15 Jan 1972, *Gillett 19528* (US, holotype; B, BR, EA, FT, K, MO, PRE, isotypes).]

Aneilema clarkei Rendle, J. Linn. Soc., Bot., 30, pl. 34: fig. 8 tantum, figs. 7, 9–12 et descr. excl. 1895.]

Aneilema calceolus Brenan, Kew Bull., 15:223, 1961 [pro *Gregory s.n*].

Annual (rarely perennial) herbs (habit types IB, IC, Figure 1; Plate 3*i*). Roots fibrous, produced only at the base and lower nodes. Primary shoot erect or ascending, much branched at the base, 15–35 cm tall, lateral shoots decumbent, or prostrate initially and then ascending. Internodes (1–)2–5(–7) cm long, green, puberulous. Leaves spirally arranged on main shoot, distichous, at least initially, on lateral shoots, sometimes becoming spirally arranged again towards the inflorescences, sheaths (1–)3–7 mm long, puberulous or pilose-puberulous, apex ciliate, laminae sessile or shortly petiolate, gradually reduced towards the terminal inflorescence on the main shoot, lanceolate or lanceolate-elliptic to ovate, 1–6.5 cm long, 0.8–2.5 (–3) cm wide, apex acute to obtuse or rounded (in smaller leaves), margin usually planar, scabrid with patent to apically directed prickle hairs, sparsely ciliate basally or on the petiole (when present), both surfaces lustrous, puberulous, adaxial with longer uniseriate hairs than the abaxial, sometimes mottled with maroon.

Inflorescences terminal on the main and major lateral shoots and on very reduced lateral shoots, ultimately produced from nearly all nodes; reduced lateral shoots frequently perforating the sheaths; larger inflorescences thyrses (Figure 53*b;* Plate 3*j*), moderately dense, broadly ovoid, 1–2(–3) cm long, 1.5–3(–5) cm wide, with up to 8 cincinni, subopposite or subverticillate

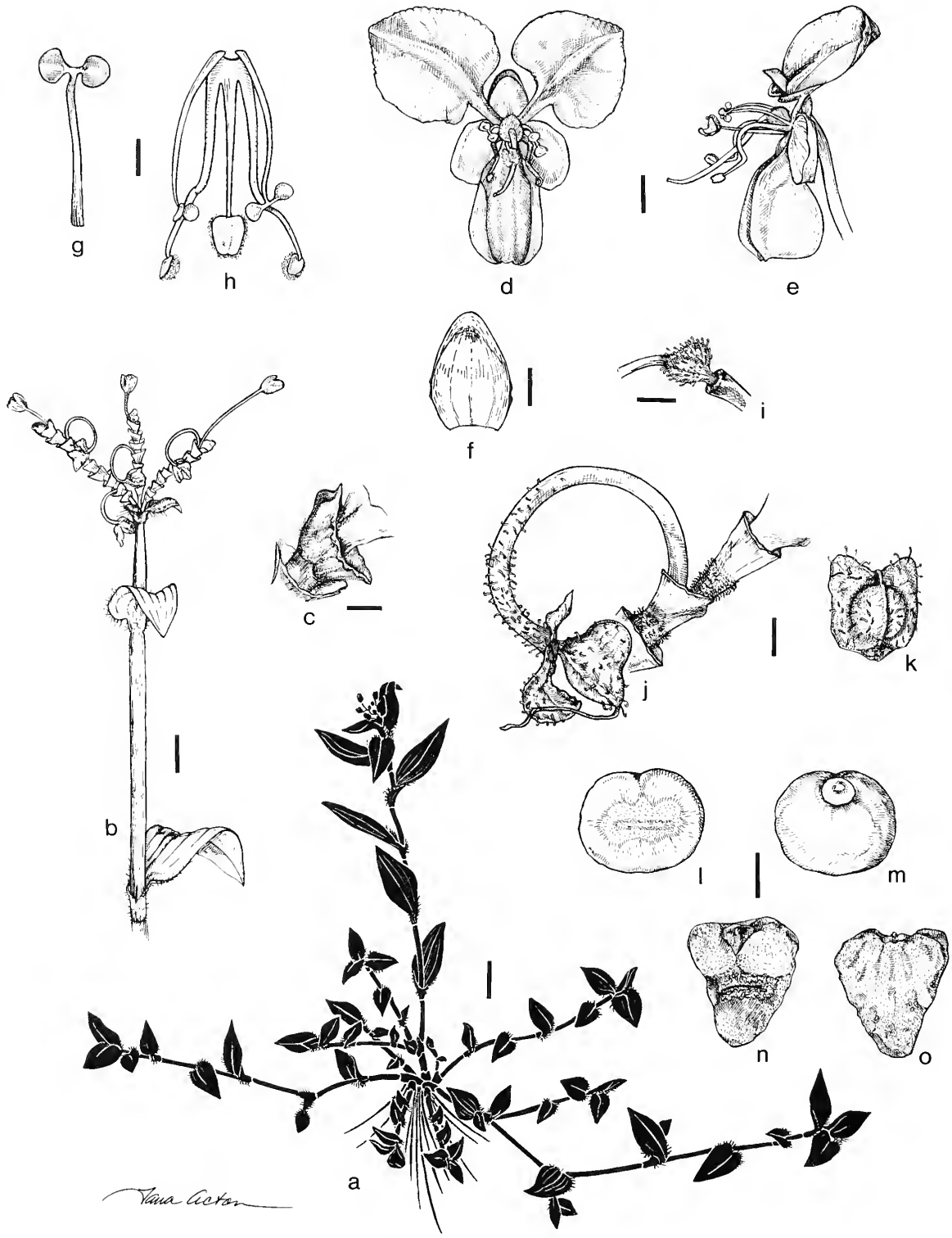


FIGURE 53.—*Aneilema tanaense* Faden: *a*, habit; *b*, inflorescence; *c*, bracteole; *d*, perfect flower, front view; *e*, perfect flower, side view; *f*, medial sepal, showing small marginal glands; *g*, lateral staminode; *h*, andoecium, top view, medial staminode omitted, gynoecium removed; *i*, ovary and base of style, side view; *j*, capsule attached to cincinnus, side view; *k*, dorsal capsule valve, dorsal view; *l*, dorsal locule seed, ventral view; *m*, dorsal locule seed, dorsal view; *n*, ventral locule seed, ventral view; *o*, ventral locule seed, dorsal view (*a*, from *Faden & Faden 74/1053; b–e,g,i*, from *Faden & Faden 77/582; f,h,j–o*, from *Gillett 19973*). (Bars = 20 mm for *a;* 5 mm for *b;* 2 mm for *d,e;* 1 mm for *c,f–k;* 0.5 mm for *l–o.*)

(occasionally some alternate), ascending; smaller inflorescences consisting of 1-several, clustered cincinni, lacking a distinct axis and not clearly thyrses. Peduncles of larger inflorescences (1–)2–5(–8.5) cm long, puberulous. Inflorescence bract supramedial to subapical, herbaceous and foliaceous. Inflorescence axis, when developed, puberulous. Cincinni to 2.2 cm long and 10-flowered (to 3.5 cm long and 17-flowered in cultivation). Cincinnus bracts herbaceous or membranous, patent or appressed to the cincinni, lanceolate to lanceolate-elliptic, ovate or oblanceolate-elliptic, 1–10 mm long, lower ones often puberulous, upper glabrous or subglabrous. Cincinnus peduncles, except the lowermost, generally exceeding the cincinnus bracts, 2–5 mm long, puberulous. Cincinnus axes puberulous. Bracteoles attached 1–2(–2.5) mm apart, ± herbaceous, symmetrically or eccentrically cup-shaped, perfoliate, 1.4–1.8 mm long, 0.8–1 mm high, prominently glandular near the apex and with smaller glands along the margin, puberulous in the basal 1/2 or, more commonly, only at the base (Figure 53*c*).

Flowers perfect and staminate, odorless, (9–)10–14.5 mm wide (Figure 53*d,e;* Plate 3*k,l*). Pedicels (4–)5.5–10(–11) mm long, erect to slightly arcuate in flower, ± uniformly recurved in fruit for their entire length 180°–270°(–360°) (Figure 53*j*), often spirally twisted as well, persistent, puberulous. Sepals prominently glandular near the apex, puberulous except for glabrous margins; medial sepal lanceolate-ovate to ovate, 2.5–3 mm long, 2–2.2 mm wide, subapical gland distinctly bilobed, smaller glands also generally present along the margin near the base (Figure 53*f*); lateral sepals elliptic to ovate-elliptic or ovate-orbicular, 2.8–3 mm long, 2–2.5 mm wide, subapical gland unlobed, marginal glands absent. Paired petals (4.2–)6.5–8 mm long, 4.8–7 mm wide, limb ovate, (2.7–)5–6 mm long, pink or pale lilac (RHS colors: 77D-78D, *Faden & Faden 74/1053;* 84B-C, 84C, *Faden & Faden 74/1185*), apex acute to obtuse or rounded, claw 1.5–2 mm long, white, glabrous. Medial petal slipper-shaped, obovate-elliptic to suborbicular or subquadrate, broadest below the margin (viewed from the apex), retaining the lateral stamens when the flower opens, 4.7–6 mm long, 3–4.7 mm wide, 3–3.6 mm deep, concolorous with the limbs of the paired petals (Figure 23*j–l;* Plate 3*k,l*). Stamen filaments fused basally and also shortly fused to lateral staminode filaments (Figures 27*a,* 53*h*). Medial staminode usually absent, rarely vestigial and represented by a short filament. Lateral staminodes with filaments 3.3–4 mm long, pink or white, shading to yellow above the middle, antherode bilobed, yellow, lobes shortly stipitate to sub-sessile, obovate-cuneate to transversely elliptic or broadly reniform, 0.3–0.8 mm long, connective not at all to scarcely elongate (Figure 53*g*). Lateral stamens with filaments ± parallel in the basal 1/2, then sharply divergent (Figures 27*a,* 53*h*), 5.5–6.5 mm long, S-shaped, geniculate and decurved in the middle, glabrous, anthers elliptic to ovate, 0.7–1.2 mm long, 0.5–0.9 mm wide, pollen yellow or orange-yellow. Medial stamen with filament 3.5–4 mm long, anther ovate, saddle-shaped, 1–1.5 mm long, 1.1–1.3 mm wide, entirely yellow, pollen yellow or orange-yellow (concolorous with lateral anther pollen). Ovary substipitate (Figure 53*i*), obovate, 1–1.2 mm long, 0.8–1 mm wide, densely and uniformly covered with patent, glandular hairs (mixed with hook-hairs along the lateral sutures), apex slightly emarginate to truncate, dorsal locule very prominent, 1-ovulate, ventral locules each 2-ovulate; style 5.5–6.5 mm long, arcuate-decurved for most of its length, also gently curving out of the floral midplane (rarely not), stigma capitate, usually held below the anthers and in front of them (Plate 3*k,l*).

Capsules (Figure 53*j,k*) substipitate to shortly stipitate, obovate (to ovate), dehiscent, bivalved, trilocular, (2.4–)2.7–3(–3.4) mm long, (1.1–)1.5–2.1 mm wide, gray to tan, sometimes with a dark gray band around the base of the dorsal locule, frequently with irregular brown spots and stripes, lustrous, puberulous, apex emarginate, dorsal valve deciduous, dorsal locule very prominent, often with a seed, ventral locules each 2-(or, by abortion, 1-)seeded, cells of the capsule wall transversely elongate. Dorsal locule seed (Figure 53*l,m;* Plate 6*g*) hemispherical, 1.1–1.6 mm long, 1–1.4 mm wide, 0.85–1 mm thick, hilum dark brown, arising from a shallow groove and flush with the flat to slightly concave ventral surface, much shorter than the seed, testa tan, smooth, lacking farinose granules and hypha-like filaments except around the hilum. Ventral locule seeds (Figure 53*n,o;* Plate 6*g*) subtriangular, apical seed rounded apically, basal seed angular basally, 1.2–1.4(–1.7) mm long, 1.2–1.3(–1.5) mm wide, 0.8–0.95 mm thick, hilum dark brown, raised within a groove, not extended onto apical and basal surfaces, testa gray or grayish tan, shallowly scrobiculate on all surfaces, sparsely white-farinose in many of the depressions and around the embryotega, densely so around the hilum, frequently some hypha-like filaments present among the farinose granules.

HABITAT.—Deciduous or semi-evergreen bushland and thickets; seasonally water-logged, gray-brown, clayey alluvium with patches of sand (Tana River District), or better drained soil (Kwale District); 10–250 m.

FLOWERING.—Flowering specimens have been seen from January, February, July, and August. The size of the largest inflorescences in *Gillett 19528* indicates that the species must have been flowering in December. Field observations show that the flowers open 0830–0900 hrs and fade 1300–1330 hrs (Figure 25).

CHROMOSOME NUMBER.—$n = 13$, $2n = 26$.

DISTRIBUTION.—Lower reaches of the Tana River and Kwale District, Kenya (Map 15).

SPECIMENS SEEN.—KENYA. KWALE: Mombasa–Nairobi road, 2.5 km towards Mombasa from turnoff of Maji ya Chumvi Railway Station, 3°49′S, 39°20′E, *Faden & Faden 77/582* (BR, EA, F, FT, K, MO, P, PRE, US, WAG); Lungalunga–Ramisi road, ~6.5 km from Vanga, 4°37′S, 39°10′E, *Faden & Faden 77/738* (EA, F, K, US); [Kilifi District on label], 5 km Maji ya Chumvi–Mackinnon Road,

3°48′S, 39°20′E, *Gilbert & Rankin 4834* (EA). TANA RIVER: 105 km N of Malindi on Garsen road, *Andrews in EA15070* (EA); Galole–Garsen road, 8 km towards Garsen from turnoff to Wenje, 1°52′S, 40°05′E, *Faden & Faden 74/1053* (C, EA, F, K, MO, US); Garsen, 2°16′S, 40°07′E, *Faden & Faden 74/1064* (EA, MO); Malindi–Garsen road, 0.8 km towards Garsen from turnoff to Kibusu, 2°21′S, 40°07′E, *Faden & Faden 74/1171* (BR, EA, K, MO, PRE, US); Garsen–Malindi road, 1.6 km towards Malindi from crossing of Lugga Buna, 2°23′S, 40°07′E, *Faden & Faden 74/1179* (EA, K, MO); Garsen–Malindi road, 1.5 km towards Malindi from turnoff to Oda, 2°32′S, 40°07′E, *Faden & Faden 74/1185* (B, BR, EA, FT, K, MO, US); Garissa–Malindi road, 16 km N of junction for Garsen, ~2°08′S, 40°04′E, *Gillett 19528* (B, BR, EA, K, MO, P, PRE, US); 105 km N of Malindi on Garsen road [Kilifi District on label], *Gillett 19532* (EA, K); Galole–Malindi road, 16 km S of spot height 106, 2°14′S, *Gillett 19973*, cultivated at Missouri Botanical Garden (BM, EA, K, MO); Lake Dumi, 13 Feb 1893, *Gregory s.n.* (BM).

DISCUSSION

The taxonomic confusion of *A. tanaense* with *A. clarkei* is explained in Faden (1984). Of the six figures that accompany the type description of *A. clarkei* (Rendle, 1895, pl. 34: figs. 7–12), Rendle's figure 8 clearly does not belong to that species. There are two separate, unmixed, Gregory collections with the same data at the British Museum (Natural History). One of them is the type of *A. clarkei* and, significantly, it has on it all of the drawings published by Rendle *except* his figure 8. The second Gregory specimen was cited by Brenan (1961) as *A. calceolus* but it is here treated as *A. tanaense*.

The first inflorescences produced by plants of *A. tanaense* are invariably distinct thyrses with a short but clear inflorescence axis. Later inflorescences consist of fewer cincinni (sometimes only one) and may lack an axis, giving them a very strong resemblance to inflorescences of *A. calceolus*. They differ from the latter chiefly in having more elongate cincinni with more widely spaced bracteoles that have glandular margins.

In Tana River District, *A. tanaense* is restricted to a peculiar type of alluvium found along the lower reaches of the Tana River. This soil type is referred to as "black cotton soil with sand" by local agricultural officers (Riyamy, personal communication). The trees and shrubs most commonly associated with *A. tanaense* are *Acacia bussei*, other *Acacia* spp., *Commiphora campestris*, *Dobera* sp., *Combretum hereroense*, *Grewia tenax*, and *Sansevieria powellii*. In Kwale District, *A. tanaense* occurs in two habitats: (1) termite mounds and thicket edge, the thickets containing trees and shrubs such as *Euclea* sp., *Diospyros consolatae*, *Manilkara* sp., *Carissa bispinosa*, *Haplocoelum inoploeum*, and *Erythroxylum emarginatum* as well as succulents; and (2) bushland and thickets dominated by *Acacia* spp. and succulents. The only two perennial populations are from the last habitat near Maji ya Chumvi.

Aneilema tanaense is transitional between the species of section *Lamprodithyros* that regularly have thyrsiform inflorescences (species 1–7) and those that never have them (species 9–13). More precisely, it is intermediate between *A. benadirense* and *A. calceolus* in lamina length, inflorescence form, cincinnus number per inflorescence, distance between bracteoles, and degree of development of marginal glands on the sepals. It agrees with both of them in fruiting pedicel curvature, medial staminode development, capsule form, and seed dimorphism. Its differences from *A. benadirense* are discussed under that species. From *A. calceolus* it differs in habit and in the characters given in the key. The close relationship between *A. tanaense* and *A. calceolus* is supported by preliminary crosses made in cultivation that suggested a high interfertility between these species.

9. *Aneilema calceolus* Brenan

Aneilema calceolus Brenan, Kew Bull., 15:223, 1961 [*Gregory s.n.* excl.]. [Type: Tanzania (Tanganyika on label), near Kange Limestone Gorge, 13 Nov 1956, *Milne-Redhead & Taylor 7285* (K, holotype; BR, EA, isotypes).]

Annual (rarely perennial) herbs (habit type IIA2, Figure 2; Plate 3*m*). Roots fibrous. Vegetative shoots repent, much branched, forming mats to 1 m or more in diameter, flowering shoots ascending, to 15(–20) cm tall. Internodes (1)2–7(–9.5) cm long, puberulous. Leaves distichous, sheaths 2–6 mm long, puberulous and generally with a few long, uniseriate hairs, particularly towards the base, ciliate at the apex, laminae sessile or shortly petiolate, ovate to ovate-elliptic or lanceolate-elliptic, 1–3.5(–5) cm long, 0.5–1.5 (–2) cm wide, apex acute or occasionally obtuse, often mucronulate, margin usually planar, scabrid with spreading to apically directed prickle hairs or short uniseriate hairs, sparsely ciliate basally or on the petiole (when present), both surfaces lustrous, puberulous, also pilose with uniseriate hairs, those on the adaxial surface longer than those on the abaxial.

Inflorescences terminal on main and lateral shoots, consisting of 1–4(–6) cincinni that appear fasciculate in the axils of 1 or 2, alternate or subopposite, sessile, foliaceous bracts or reduced leaves; inflorescences actually reduced thyrses (see discussion below), to ~2 cm long and wide. Peduncles to 7.5 cm long, puberulous. Inflorescence bract apical or subapical, herbaceous, foliaceous, often only slightly smaller than the leaf at the node below. Inflorescence axis ± not developed. Cincinni (when more than 1) subopposite or subverticillate, ascending or becoming arcuate with age, to 7 mm long and 14-flowered (to 11 mm long and 25-flowered in cultivation). Cincinnus bracts herbaceous and green (the lowermost generally so) or membranous and whitish or brownish, lower ones patent, others appressed to the cincinni, lanceolate-elliptic to ovate, up to 13 mm long (much smaller in the upper cincinni), not evidently glandular (at least the lower ones), puberulous to glabrous. Cincinnus peduncles not developed. Cincinnus axes

very short, generally completely covered by overlapping bracteoles, glabrous. Bracteoles attached 0.2–1(–1.4) mm apart, membranous, slightly to strongly eccentrically cup-shaped, perfoliate, 1.1–1.9 mm long, 0.4–1 mm high, inconspicuously glandular near the apex, glabrous or subglabrous.

Flowers perfect and staminate, odorless, (10–)12–15 mm wide (Plate 3*n,o*). Pedicels 7–11 mm long in flower, to 13(–16?) mm in fruit, ± erect in flower, sometimes slightly arcuate near the apex, ± uniformly recurved in fruit for their entire length generally ~270°, frequently somewhat spirally twisted as well, persistent, puberulous except at the base (Figure 35*c*). Sepals glandular near the apex, puberulous; medial sepal lanceolate to ovate-elliptic, 3–4 mm long, 2–2.5 mm wide, gland inconspicuously bilobed; lateral sepals ovate-elliptic to ovate, 3–4 mm long, 2.5–2.7 mm wide, gland inconspicuous (sometimes absent?), unlobed. Paired petals 5–9 mm long, 3.5–7.5 mm wide, limb ovate, lilac (RHS colors: 76B, *Organ in EA14970*, cultivated; 76C, *Faden & Faden 74/324*, cultivated; 84C, *Faden & Faden 74/1069*), apex rounded or obtuse to subacute, claw 1–3 mm long, whitish, glabrous. Medial petal slipper-shaped, elliptic to obovate-elliptic, somewhat keeled medially, broadest below the involute margin (viewed from the apex), retaining the lateral stamens when the flower opens, 5–7.5 mm long, 2.5–4 mm wide, ~2.5–3.7 mm deep, concolorous with the limbs of the paired petals (Figure 23*m–o;* Plate 3*n,o*). Lateral stamen filaments fused basally to medial stamen filament and sometimes to lateral staminode filaments (Figure 27*b*). Medial staminode absent, or rarely represented by a short filament. Lateral staminodes with filaments 2.5–3.5 mm long, white basally, shading to yellow above the middle, antherodes bilobed, yellow, lobes stipitate, transversely elliptic to broadly ovate, subreniform or obovate-cuneate, 0.4–0.7 mm long, connective not elongate. Lateral stamens with filaments parallel or divergent in basal 1/3, more strongly divergent in middle 1/3, less divergent to almost parallel in apical 1/3 (Figure 27*b*), 4–8 mm long, S-shaped, geniculate and decurved near the middle, glabrous, anthers elliptic to ovate, 0.7–1.25 mm long, 0.5–0.75 mm wide, pollen white. Medial stamen with filament 3–5 mm long, anther lanceolate-ovate to ovate, saddle-shaped, 1.4–2 mm long, 1.2–1.5 mm wide, pollen yellow. Ovary substipitate, obovate, 0.9–1 mm long, 0.9–1.1 mm wide, densely and uniformly covered with patent, glandular hairs (mixed with hook-hairs along the lateral sutures), apex truncate to slightly emarginate, dorsal locule very prominent, 1-ovulate, ventral locules each 2-ovulate; style 5.5–7 mm long, very gently arcuate-decurved at least 1/2 of its length, then recurved towards the apex, also gently curved laterally out of the floral midplane, stigma slightly capitate, held in front of the anthers and vertically between the levels of the medial and lateral anthers.

Capsules (Figure 35*c,d*) substipitate, obovate, dehiscent, bivalved, trilocular, (2.3–)2.5–3.6 mm long, (1.4–)1.9–2.5 (–2.8) mm wide, ± carinate middorsally, light brown or pale grayish brown, spotted and striped with dark brown, lustrous, puberulous, apex emarginate, dorsal valve deciduous, dorsal locule very prominent, usually with a seed, ventral locules each 2-(or, by abortion, 1-)seeded, cells of the capsule wall transversely elongate. Dorsal locule seed (Plate 6*f*) hemispherical, 1.2–1.6 mm long, 1–1.4 mm wide, 0.8–1.1 mm thick, hilum dark brown, arising from a shallow groove, much shorter than the seed, testa tan, smooth, lacking farinose granules or with farinose granules sparse around the embryotega and ± dense around the hilum where sometimes mixed with hypha-like filaments. Ventral locule seeds (Figure 38; Plate 6*f*) subtriangular, apical seed obtuse to rounded apically, basal seed angular basally, 1.2–1.6(–2) mm long, 1.1–1.5 mm wide, 0.7–1 mm thick, hilum dark brown, raised within a groove, not extended onto apical and basal surfaces, testa tan, pinkish tan or grayish tan, shallowly scrobiculate on all surfaces, usually white-farinose in most of the depressions and around the embryotega and hilum, frequently some hypha-like filaments present among the farinose granules (Figure 38*d*).

HABITAT.—Dry or moist, lowland evergreen forest or thicket; growing on Kambe limestone, often in shallow soil, in the Tanga area of Tanzania; partial or dense shade; 10–450 m.

FLOWERING.—Flowering specimens have been seen from June, July, and September–November. Field observations of *Faden & Faden 74/1069* indicate that the flowers open 0900–1000 hrs and fade 1300–1330 hrs (Figure 25).

CHROMOSOME NUMBER.—$2n = 26$.

DISTRIBUTION.—Coastal Kenya and Tanzania (Map 15).

SPECIMENS SEEN.—KENYA. KWALE: Lungalunga–Ramisi road, 1 km before turnoff to Kinango, 4°32′30″S, 39°05′30″E, *Faden & Faden 77/378* (BR, EA, F, K, MO, PRE, US, WAG). TANA RIVER: Garsen–Witu road, near Nyangoro Bridge, 2°18′S, 40°20′E, *Faden & Faden 74/1069* (EA, K, MO, US); same locality, *Faden & Faden 77/565* (EA, F, K, US).

TANZANIA. TANGA: Amboni Cave near Tanga, 5°04′S, 39°03′E, *Botany Students in DSM1351* (EA); 5 mi SE of Ngomeni, *Drummond & Hemsley 3561* (B, BR, EA, K, LISC, S); Amboni Caves ~2 km E of Tanga, ~5°06′S, 39°03′E, *Faden & Faden 74/324* (EA, K, MO, US); Kange Gorge, ~5 km E of Tanga, ~5°06′S, 39°01′E, *Faden & Faden 74/333* (EA, F, K, PRE, US, WAG); Usambara foot-hills, Maramba Forest, *Faulkner 4045* (K); 2 mi N of Tanga, *Harris & Procter 1018* (EA); near Kange Limestone Gorge, *Milne-Redhead & Taylor 7285* (BR, EA, K); Kiomoni Quarries near Tanga, cultivated in Nairobi, *Organ in EA14970* (EA).

DISCUSSION

Gregory s.n. cited by Brenan (1961) as this species differs from the Tanzanian specimens in being more erect and in having shorter pedicels, more elongate cincinnus axes that are puberulous where exposed, and especially in its bracteoles with small glands along the margin and generally sparsely puberu-

lous. It also has small marginal glands on the medial sepal. This specimen is treated above as *A. tanaense*.

Aneilema calceolus is generally annual. Only completely or nearly completely dead plants of *Faden & Faden 74/324, 74/333,* and *77/378* were found in the field, and *74/324* and *77/378,* when grown from seed, behaved as annuals, i.e., after flowering and fruiting they ceased vegetative growth and were unable to root from cuttings. However, the northernmost, isolated population in the Tana River District of Kenya (*Faden & Faden 74/1069* and *77/565*) is definitely perennial and has been cultivated for more than ten years.

The inflorescence of *A. calceolus* is easily interpreted as a reduced thyrse in which the inflorescence axis and cincinnus peduncles are suppressed and the cincinnus axes are very contracted. When the lowermost cyme appears to be separated from the others, a short inflorescence axis thus seemingly present, careful observations of the sequence of flowering usually indicates that this cyme does not flower until after the one above it. This "lowermost" cincinnus is therefore an entire inflorescence consisting of a single cincinnus axillary in the inflorescence bract, while the cincinnus above that one is morphologically the true lowermost one of the terminal inflorescence.

In inflorescences that consist of a subopposite pair of terminal, leaf-like bracts, each subtending a cincinnus, again the cincinnus of the larger, lower bract does not flower until after that of the upper one. The lower cincinnus in this case must also be considered an entire inflorescence axillary in the inflorescence bract. The true terminal inflorescence also consists of a single cincinnus.

In *A. calceolus* the stamens are retained by the medial petal longer than in any other species of section *Lamprodithyros* (Figure 25). Field observations of *Faden & Faden 74/1069* indicate that the stamens are held for an average of two and one-third hours or approximately half of the flowering period.

The habitat requirements of *A. calceolus* appear to fall within the range of those for *A. clarkei,* with which it is sympatric. The two have never been found growing together, although each has been collected with or near *A. taylorii* on very similar outcrops of Kambe limestone. There is no obvious reason for their apparent mutual exclusion; competition for space should be considered as a possible factor.

Aneilema calceolus differs from *A. clarkei,* with which it was contrasted by Brenan (1961), by the former's having usually an annual habit, blunter laminae, often several cincinni per inflorescence, fruiting pedicels uniformly recurved for their entire length and puberulous for most of their length (versus recurved and puberulous only at the apex), much smaller, lilac petals, usual absence of a medial staminode, smaller capsules with a deciduous dorsal valve, and smaller, more dimorphic seeds. *Aneilema calceolus* also differs from *A. lamuense* and *A. succulentum* in inflorescence structure, pedicel curvature and pubescence, medial petal shape (Figures 23*m–o*, 24*d–i*) and lack of a medial staminode. It is clearly less closely related to these species than they are to each other or to *A. clarkei.*

The most closely related species to *A. calceolus* is *A. tanaense*. They agree in flower and capsule structure, pedicel curvature and pubescence, and seed dimorphism. Reduced inflorescences of *A. tanaense* are very similar to inflorescences of *A. calceolus*. The two species differ in habitat, habit, and in the characters given in the key.

10. *Aneilema clarkei* Rendle

Aneilema clarkei Rendle, J. Linn. Soc., Bot., 30:430, pl. 34: figs. 7, 9–12 [non fig. 8], 1895.—Schumann in Engler, Pflanzenwelt Ost-Afrikas C, 136, 1895.—Clarke in Thiselton-Dyer, Fl. Trop. Africa, 8:73, 1901.—Brenan, Kew Bull., 15:224, 1961 [in adnot.]. [Type: Kenya, Tana [River District], Lake Dumi, 13 Feb 1893, *Gregory s.n.* (BM)]

Perennial herbs (habit type IIA2, Figure 2). Roots fibrous. Vegetative shoots procumbent to repent, much branched; flowering shoots erect to ascending, generally unbranched, 15–30(–40) cm tall. Internodes (1–)1.5–7(–13) cm long, glabrous to puberulous. Leaves distichous (the 2 ranks at an obtuse angle to each other), usually gradually reduced apically on the flowering shoots, sheaths 2.5–10 mm long, puberulous and generally sparsely pilose with uniseriate hairs, particularly at their bases, apex ciliate, laminae petiolate, lanceolate to linear-lanceolate, lanceolate-elliptic or ovate, 1.5–5(–7.8) cm long, (0.4–)0.8–1.5(–2.5) cm wide, apex acuminate to acute, margin usually planar (occasionally somewhat undulate), scabrid, sparsely ciliate basally or on the petiole (when present), both surfaces lustrous, pilose-puberulous, the uniseriate hairs of the adaxial surface longer and generally fewer than those of the abaxial surface.

Inflorescences terminal on the flowering shoots and also on short, non-perforating shoots produced from the uppermost 1–3 nodes on the flowering shoots, each inflorescence consisting of a short, solitary cincinnus subtended by and partially enclosed in a subopposite pair of herbaceous (or occasionally the upper or both membranous) bracts, the larger, lower one the inflorescence bract, the upper the cincinnus bract (Figure 9; Plate 3*p*). Peduncles ~0–2.5 cm long, puberulous. Inflorescence bract terminal, herbaceous or rarely membranous. Cincinni to ~5 mm long and 10-flowered. Cincinnus bracts herbaceous or rarely membranous, lanceolate, often falcate, ascending, ~5.5–15 mm long (including the sheath) × 3–5 mm wide, eglandular, both surfaces puberulous, adaxial also densely pilose, margins longly ciliate, at least towards the apex. Cincinnus peduncles not developed. Cincinnus axes very short, completely covered by overlapping bracteoles, glabrous (Figure 35*e*). Bracteoles attached up to 0.2 mm apart, membranous, slightly to strongly eccentrically cup-shaped, perfoliate, ~3–5 mm long × 2 mm high, apparently eglandular, lower (outer) ones sparsely puberulous with uniseriate hairs and often hook-hairs, upper (inner) ones apparently glabrous.

Flowers perfect and staminate, odorless, (12.5–)15–20 mm wide (Plate 4*d*). Pedicels 7–11.5 mm long, arcuate-erect to

gently S-shaped in flower, in fruit, strongly recurved (~180°-270°) only near the apex and becoming much thickened in that region (Figure 35*e*), persistent, greenish white, puberulous generally only near the apex, rarely extending to below the middle. Sepals glandular near the apex, glands unlobed; medial sepal lanceolate-ovate to ovate-deltate, 3.2-5 mm long, 2.5-4.5 mm wide, glabrous, or sparsely puberulous basally; lateral sepals ovate-elliptic to broadly ovate or ovate-orbicular, 3.3-5.5 mm long, 2.7-4.5 mm wide, sparsely puberulous medially and basally. Paired petals (7.5-)9-12 mm long, (5.5-)7-11 mm wide, limb ovate to ovate-deltate or ovate-subreniform, ~5-8 mm long, lilac to lavender (RHS colors: 87D, *Faden & Faden 74/1215*, field & cultivated, & *Faden & Faden 72/226A*, cultivated; 85C, 87C-D, *Evans & Maikweki 51*, cultivated; 88D, *Faden et al. 71/633*, cultivated), apex obtuse to rounded, margin crenulate to subentire, claw 2.5-4 mm long, white or concolorous with limb (always paler at the base), glabrous. Medial petal cup-shaped, ovate, broadest at the margin (viewed from the apex), which is frequently slightly revolute, nearly always retaining the lateral stamens when the flower opens, 6-9 mm long, 3-7 mm wide, 2.5-5 mm deep, concolorous with the limbs of the paired petals, paler basally, (Figure 24*a-c*; Plate 4*d*). Lateral stamen filaments fused basally to medial stamen filament and to the lateral staminode filaments (Figure 28*a*). Medial staminode (rarely absent) filament 0.7-2 mm long, entirely yellow or white, or pinkish purple basally, antherode bilobed, yellow, lobes sessile, ovate to suborbicular, reniform or transversely elliptic, 0.4-0.8 mm long, connective slightly elongate. Lateral staminodes with filaments 3-5 mm long, lilac to lavender basally, shading to yellow in the apical $^1/_3$-$^1/_2$, antherodes bilobed, yellow, lobes subsessile to shortly stipitate (rarely sessile), transversely elliptic to broadly ovate-cuneate or obovate-cuneate, 0.7-0.8 (-1) mm long, connective slightly to not at all elongate. Lateral stamens with filaments divergent (Figure 28*a*), (5.5-)6.5-8.5 mm long, S-shaped, geniculate and decurved near the middle, glabrous, anthers lanceolate-elliptic to broadly elliptic or ovate, 1-1.6 mm long, 0.5-1.1 mm wide, pollen white. Medial stamen with filament 3.5-5.5 mm long, anther ovate-elliptic to oblong, saddle-shaped, 1.4-2.5 mm long, 1-1.6 mm wide, pollen yellow. Ovary substipitate, obovate to obovate-oblong or obovate-elliptic, (1-)1.5-1.9 mm long, (1-)1.1-1.3 mm wide, densely and uniformly covered with patent, glandular hairs, usually mixed with few to many hook-hairs (best seen in fruit) (Figure 42*i,j*), apex truncate to rounded or slightly emarginate, dorsal locule very prominent, 1-ovulate, ventral locules each 2-ovulate; style 7.5-11 mm long, nearly straight or gently arcuate-decurved for most of its length, recurved near the apex, also gently curved out of the floral midplane, stigma capitate, violet, held in front of the anthers and generally below them.

Capsules (Figure 35*e*) substipitate, obovate to oblong-elliptic, dehiscent, bivalved, trilocular, 3.6-4.5 mm long, 2.3-3 mm wide, tan or grayish tan, with small, dark brown spots, particularly around the base of the dorsal locule, lustrous, puberulous, apex truncate to emarginate, valves persistent or dorsal valve tardily deciduous, dorsal locule very prominent, 1-seeded (or occasionally empty), ventral locules each 2-(or, by abortion, 1-)seeded, cells of the capsule wall transversely elongate. Seeds (Plate 6*h*) broadly elliptic, 1.8-2 mm long, 1.4-1.5 mm wide (dorsal locule seed) or ovate to subtriangular, with apical seeds rounded apically and basal seeds angular basally, 1.5-1.7(-2.1) mm long, 1.5-1.6 mm wide (ventral locule seeds), 0.9-1.1 mm thick, hilum dark brown, prominently raised within a groove, not extended onto apical and basal surfaces, testa light brown, shallowly scrobiculate on the dorsal surface, sparsely white-farinose in some of the depressions, densely so around the embryotega and hilum.

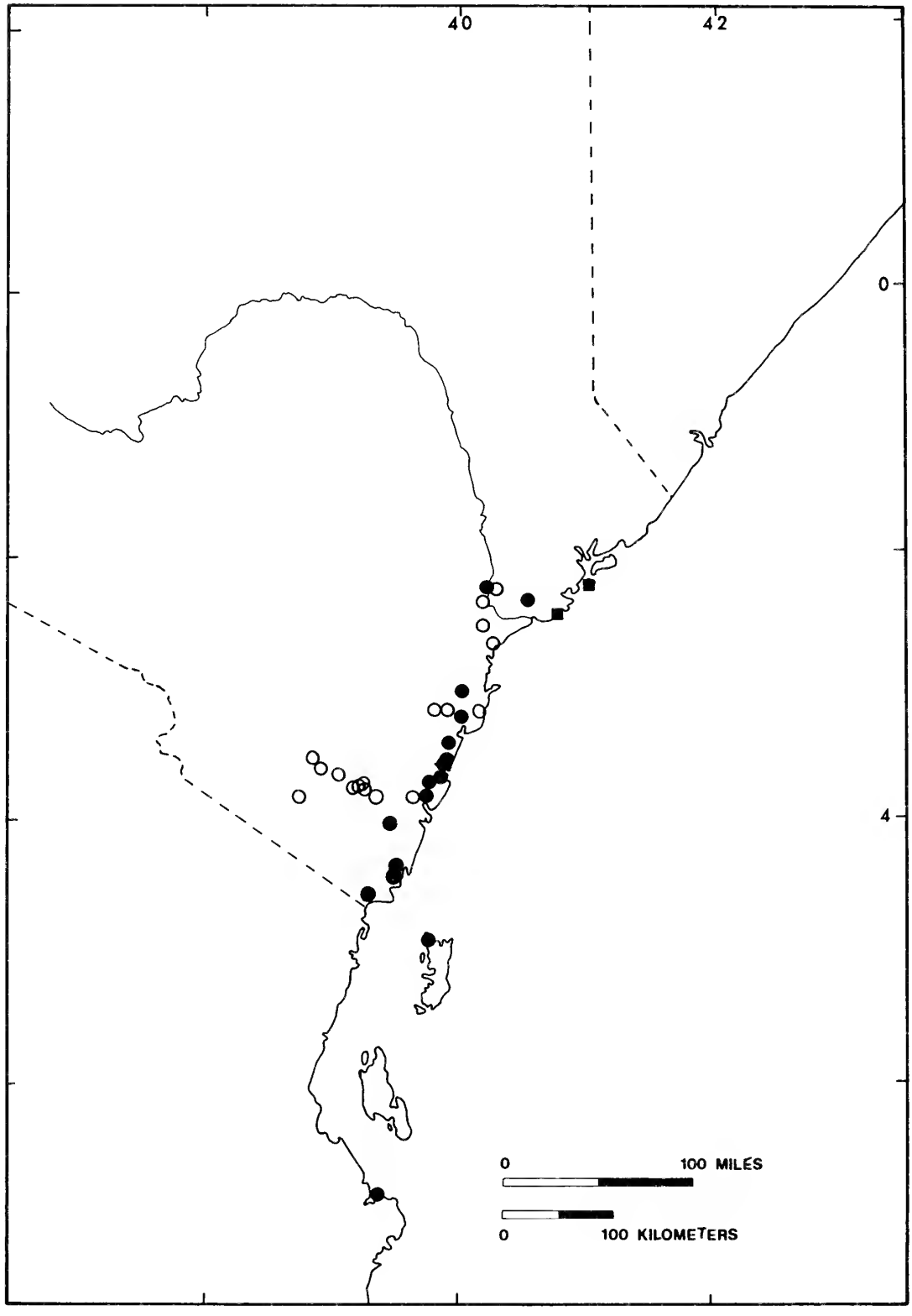
HABITAT.—Lowland evergreen forest (sometimes on Kambe limestone), *Brachystegia* forest or woodland on tan sand, river slopes, *Hyphaene-Albizia* scrub on sand, and moist thickets; dense or partial shade; 0-220 m.

FLOWERING.—Flowering specimens have been seen from January to March, May, and July-November. Field observations of three populations indicate that the flowers open 0845-0930 hrs and fade 1200-1300 hrs.

CHROMOSOME NUMBER.—$2n = 78$.

DISTRIBUTION.—Coastal Kenya and Tanzania (including Pemba Island) (Map 16).

SPECIMENS SEEN.—KENYA. KILIFI: Sokoke-Arabuko Forest on Malindi-Mombasa road, just N of 50 mi sign, *Evans & Maikweki 51* (EA); Pangani Forest at crossing of Lwandani Stream on Ribe-Chonyi road, 3°52′S, 39°40′E, *Faden & Beentje 85/49* (US); Sokoke Forest, road to Jilore Forest Station, 3.2 km from turnoff on Kilifi-Malindi road, *Faden & Evans 71/714* (DSM, EA, K, MO, US, WAG); Chasimba, Kaloleni-Kilifi road ~14 km, 3°43′S, 39°42′E, *Faden & Evans 71/726* (EA, K); same locality, *Faden & Faden 71/788* (C, EA, FT, K, MO, PRE, US); Sokoke Forest, 21.3 km S of Gede turnoff, ~3°26′S, 39°53′E, *Faden et al. 71/633* (BR, C, EA, F, G, K, MO, PRE, US, WAG); Mnarani, S side of Kilifi Creek, *Faden & Faden 71/809* (B, BR, EA, FT, K, LISC, MO, P, PRE, US, WAG); 1 km NE of Pangani on Chonyi-Ribe road, 3°52′S, 39°40′E, cultivated Missouri Botanical Garden, *Faden & Faden 72/226A* (BR, EA, K, MO); Sokoke Forest, ~3 km on track S of Gede to Jilore Forest Station, ~3°18′S, 39°57′E, *Faden & Faden 74/1215* (BM, EA, K, MO); Pangani, crossing of Lwandani Stream on Chonyi-Ribe road, 3°51′S, 39°41′E, *Faden et al. 77/523* (EA); Kilifi, *Jeffery K315* (EA, G, K); Marafa, 25 mi NW of Malindi, *Polhill & Paulo 796* (BR, EA, K, PRE). KWALE: Mwachi Forest, N end, along Mwachi River, 3°59′30″S, 39°32′30″E, *Faden & Faden 77/484* (EA); N side of Gogoni Forest, ~4°24′S, 39°28′E, *Faden & Faden 77/629* (US); Mwena River S of Marenje Forest, N side of river, 4°32′S, 39°12′E, *Faden & Faden 77/749* (BR, EA, F, K, MO, US, WAG); Muhaka Forest, N end, 4°20′S, 39°31′E, *Faden & Faden 77/775* (EA, US). LAMU: Mambasasa, Utwani Forest Reserve, *Greenway & Rawlins 9344* (EA, K). TANA RIVER:



MAP 16.—Distribution of *Aneilema clarkei* Rendle (solid circles), *A. lamuense* Faden, new species (solid squares), and *A. succulentum* Faden, new species (open circles).

Lake Dumi, 13 Feb 1893, *Gregory s.n.* (BM).

TANZANIA. UZARAMO: Near Magogoni, *Vaughan 2395* (EA). PEMBA: Ngezi Forest, *Vaughan 621* (EA, K) & *2064* (BM).

DISCUSSION

Rendle's figure 8, which accompanied the type description of *A. clarkei*, is not of this species but of *A. tanaense*. Gregory collected the latter the same day he collected the type of *A. clarkei*. The remaining figures published by Rendle do belong to *A. clarkei* and are reproduced from drawings on the type specimen. Only Rendle's figure 8 is not on the type (see discussion under *A. tanaense*).

Plants of *A. clarkei* tend to form mats where locally common. Vegetative shoots can attain at least one meter in length.

Clarke (1901) observed that the leaves in this species were "somewhat polymorphic." While they are in fact no more so than in many other *Aneilema* species, several factors combine to make this polymorphism more obvious in *A. clarkei*. The relatively short flowering shoots have towards their bases the usual transition from prophyll to mature leaf. In addition, the leaves are generally reduced towards the terminal inflorescence. Thus in a moderately short flowering shoot there may be two transitions in lamina size and shape. The net effect is that leaf shape polymorphism is more concentrated, hence more striking, in *A. clarkei* than in most other species in the genus.

Every cincinnus in *A. clarkei* is the homolog of an entire thyrse. This is evidenced by the presence of two bracts at the base of the cincinnus, the larger, lower one the inflorescence bract, the upper the cincinnus bract (Figure 9). The uppermost cincinnus is the terminal inflorescence; it lacks the basal prophyll that characterizes the other, lateral cincinni, and lateral shoots in general.

Two cincinni are frequently closely associated at the end of the flowering shoot, suggesting a larger inflorescence unit than the single cincinnus proposed here. In these examples the true terminal cincinnus has just the two bracts associated with it, while the subterminal, sessile, or subsessile cincinnus appears to have four. The lowermost of these is a foliage leaf. The next, visible only upon dissection, is a prophyll. The upper two are homologous to the two bracts of the terminal cincinnus. The prophyll indicates that the subterminal cincinnus is actually terminal on a very reduced lateral shoot and is not a part of the same thyrse as the terminal cincinnus. Of course, the two cincinni may be functionally related—as in the attraction of pollinators by simultaneously producing flowers—but their morphological relationship is equivalent to the loose association of thyrses found at the ends of the flowering shoots in many *Aneilema* species.

The retention of the lateral stamen filaments by the middle petal is a well-developed and nearly constant character in *A. clarkei*. Field notes on *Faden & Faden 71/809* indicate that in a rare flower the stamens are not held. Also rarely, one stamen is not released.

The presence of dorsal capsule valves in mature fruiting specimens of *A. clarkei* shows that this valve is not regularly deciduous. The same interpretation has been used for other species in section *Lamprodithyros*, such as *A. recurvatum* and *A. zebrinum*. These conclusions are supported by observations of these species in cultivation. In contrast, the dorsal capsule valves in other species of this section, such as *A. calceolus*, *A. lamuense*, and *A. petersii*, are usually deciduous. The dehiscence of the dorsal valve, or lack thereof, is probably related to seed dispersal (see p. 38).

Aneilema clarkei occurs in a variety of habitats. All of them are similar in having at least 760 mm rainfall (*National Atlas of Kenya*, 1970) and probably calcareous soils.

Aneilema clarkei is readily distinguished from *A. calceolus*, with which Brenan (1961) contrasted it, by its inflorescence structure, distinctly perennial habit, pedicels recurved and puberulous only near the apex, larger and bluer flowers that nearly always have a medial staminode, and larger capsules in which the dorsal valve is often persistent.

Similar inflorescence structure and fruiting pedicel curvature to those of *A. clarkei* are found only in *A. succulentum* and *A. lamuense*, which must be considered its closest relatives. The three species may be worth treating as a series within section *Lamprodithyros*, but further studies are required of other species before the section can be satisfactorily subdivided. *Aneilema clarkei* differs from *A. succulentum* by the former's petiolate leaves with symmetric bases and larger capsules and seeds, from *A. lamuense* by its perennial habit, lack of uniseriate hairs on the pedicels and sepals, and yellow medial anther with yellow pollen, and from both in its larger, bluer flowers, better-developed stamen-retention mechanism, more divergent lateral stamen filaments, and less regularly deciduous dorsal capsule valves.

11. *Aneilema lamuense* Faden, new species

Herbae annuae foliis sessilibus vel breviter petiolatis, spiraliter dispositis vel distichis laminis ovato-ellipticis ad ovatas, lanceolatas vel lanceolato-ellipticas, (1–)2–4.5(–5.8) cm longis, 1–2(–2.5) cm latis. Inflorescentiae terminales in caule principali caulibusque lateralibus principalibus etiam in caulibus brevibus e nodis 1–3 summis caulium principalium prodientibus, cincinnis brevibus solitariis jugo bractearum subtentis et partim inclusis compositae. Pedicelli 7–10 mm longi, in fructu valde recurvati (~180°) tantum prope apicem, piloso-puberuli prope apicem. Petalum medium cymbiforme vel cupulatum. Antherae omnes 3 pollen album continentes. Capsulae 3.6–4.3(–5) mm longae, 1.95–2.1(–2.55) mm latae, valva dorsali decidua, loculo dorsali 1-seminali, loculis ventralibus uterque 2-seminalibus. Semina loculorum ventralium ovata vel subtriangularia, (1.35–) 1.45–1.7(–1.8) mm

longa, 1.4–1.75 mm lata, testa scrobiculata non profunda vel sulcato-scrobiculato (Figure 54).

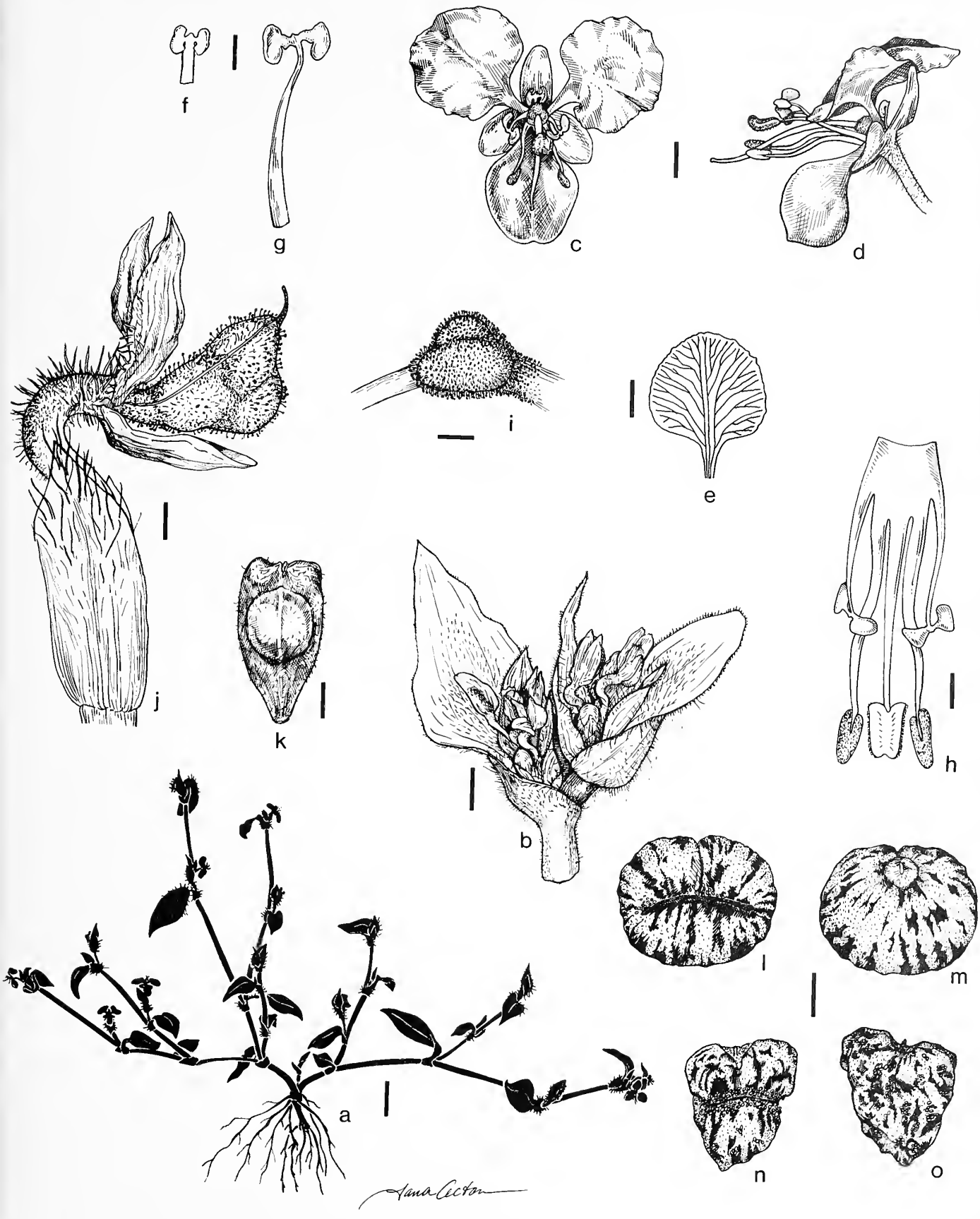
TYPE.—Kenya, Lamu District [Tana River District on label], Kitwa Pembe Hill and vicinity, 2°27′S, 40°42′E, 15–16 Jul 1974, *Faden & Faden 74/1083* (US, holotype; BR, C, EA, FT, K, MO, PRE, UPS, isotypes).

Annual herbs (habit type IC, or occasionally IIIA, Figures 1, 54*a;* Plate 4*a*). Roots fibrous. Shoots erect to ascending or sometimes decumbent, usually much branched, to ~20(–40) cm tall, all shoots eventually terminating in inflorescences. Internodes (0.5–)1.5–6(–9) cm long, puberulous (sometimes only just below the nodes). Leaves spirally arranged on the main shoot, distichous (the 2 ranks at an obtuse angle to each other) on the lateral shoots (only ~4–5 leaves produced on the larger lateral shoots), not reduced towards the terminal inflorescence, sheaths 3–9 mm long, puberulous and usually with a few uniseriate hairs (lower leaves) or densely pilose-puberulous (uppermost leaves), apex ciliate, laminae shortly petiolate or sessile, ovate-elliptic to ovate, lanceolate or lanceolate-elliptic, (1–)2–4.5(–5.8) cm long, 1–2(–2.5) cm wide, apex acute to acuminate, margin usually planar, scabrid, sparsely ciliate basally or on the petiole (when present), adaxial surface dull, abaxial lustrous, both surfaces pilose-puberulous, the uniseriate hairs longer on the adaxial surface than the abaxial.

Inflorescences (Figure 54*b*) terminal on the main shoots and also on short, non-perforating shoots produced from the uppermost 1–3 nodes on the main and major lateral shoots (sometimes also terminal on more elongate, ± leafy shoots produced from lower nodes), each inflorescence consisting of a short, solitary cincinnus subtended by and partially enclosed in a subopposite pair of herbaceous bracts, the larger, lower one the inflorescence bract, the upper the cincinnus bract. Peduncles to ~1 cm long, puberulous. Inflorescence bract terminal, herbaceous. Cincinni to ~5 mm long and 10-flowered. Cincinnus bracts herbaceous, lanceolate, falcate, erect to ascending, ~8–20 mm long (including the sheath) × 2–5 mm wide, eglandular, both surfaces pilose-puberulous, margins longly ciliate. Cincinnus peduncles not developed. Cincinnus axes very short, completely covered by overlapping bracteoles, glabrous. Bracteoles attached up to 0.2 mm apart, membranous, lanceolate-ovate to ovate, often eccentrically cup-shaped, perfoliate or not, ~4–6 mm long, to ~2 mm high, eglandular but the apex thickened, lower (outer) ones pilose-puberulous, upper (inner) ones pilose only at the apex or completely glabrous.

Flowers perfect and staminate, odorless, 10.5–14(–15.5) mm wide (Figure 54*c,d;* Plate 4*b,c*). Pedicels 7–10 mm long, arcuate-erect to gently S-shaped in flower, in fruit, strongly recurved (~180°) only near the apex and becoming much thickened in that region, persistent, pilose-puberulous near the apex, otherwise glabrous (Figure 54*j*). Sepals not clearly glandular; medial sepal lanceolate to lanceolate-ovate or lanceolate-elliptic, 2.8–3.6 mm long, 1.6–2.1 mm wide, generally glabrous, occasionally sparsely puberulous at the base; lateral sepals elliptic to obovate-elliptic or ovate-elliptic, 3.5–4.3 mm long, 2–2.6 (–2.9) mm wide, pilose-puberulous along the basal 1/2 of the medial (lower) edge, the long, uniseriate hairs very few. Paired petals (Figure 54*e*) 6–9 mm long, 5-7(–8) mm wide, limb ovate 4–5.5(–6) mm long, lilac (RHS color: 81C, C-D, D, *Faden & Faden 74/1083*), apex acute to obtuse or rounded, margin crenulate, claw 2–3 mm long, concolorous with limb apically, whitish basally, glabrous. Medial petal boat or cup-shaped, ovate, broadest at the margin (viewed from the apex), retaining the lateral stamens when the flower opens, 5–6(–7.5) mm long, 2–4.5(–6) mm wide, 2.8–3.7(–3.9) mm deep, whitish except basally where ± concolorous with the limbs of the paired petals (Figure 24*d-f*). Lateral stamen filaments fused basally to medial stamen filament and lateral staminode filaments (Figures 28*c,d,* 54*h*), stamen filaments shortly adnate to medial petal base. Medial staminode filament 0.3–1(–1.5) mm long, pinkish purple, antherode bilobed, lobes sessile or subsessile, broadly ovate to reniform, 0.5–0.7 mm long, yellow with pinkish purple bases, connective slightly elongate (Figure 54*f*). Lateral staminodes with filaments 3.5–4.7 mm long, ventrally displaced, lilac, shading to white near the apex, antherodes bilobed, lobes stipitate, obovate to broadly ovate, reniform or transversely elliptic, 0.45–0.65 mm long, yellow with a pinkish purple or violet, cuneate base, connective very slightly elongate (Figure 54*g*). Lateral stamens with filaments parallel in the perfect flowers, divergent above the middle (and somewhat longer) in the staminate flowers (Figures 28*c,d,* 54*h*), (5–)6–8.5 mm long, ± S-shaped, decurved about the middle, glabrous, anthers lanceolate-elliptic to elliptic, 1.4–1.7 mm long, 0.8–1 mm wide, pollen white. Medial stamen with filament 4.5–6(–6.3) mm long, anther lanceolate to oblong, saddle-shaped, 1.6–2 mm long, 1–1.35 mm wide, entirely creamy white, pollen white. Ovary substipitate (Figure 54*i*), obovate-elliptic to obovate, 1.5–1.75 mm long, 1–1.2 mm wide, densely and uniformly covered with patent, glandular hairs (mixed with some hook-hairs, best seen in fruit), apex rounded to truncate, dorsal locule very prominent, 1-ovulate, ventral locules each 2-ovulate; style 7–8 mm long, nearly straight to gently arcuate-decurved for most of its length, also gently curved out of the floral midplane, sometimes with a few hook-hairs and/or glandular hairs near the base, stigma capitate, held slightly in front of the anthers and generally at the same level as them.

FIGURE 54.—*Aneilema lamuense* Faden, new species: *a*, habit; *b*, end of flowering shoot showing terminal inflorescence and uppermost lateral inflorescence; *c*, perfect flower, front view; *d*, perfect flower, side view; *e*, paired petal; *f*, medial staminode; *g*, lateral staminode; *h*, androecium of perfect flower, top view, medial staminode omitted, gynoecium removed; *i*, ovary and base of style, side view; *j*, capsule attached to cincinnus, side view; *k*, dorsal capsule valve, dorsal view; *l*, dorsal locule seed, ventral view; *m*, dorsal locule seed, dorsal view; *n*, ventral locule seed, ventral view; *o*, ventral locule seed, dorsal view (all from *Faden & Faden 74/1083*). (Bars = 20 mm for *a;* 4 mm for *b;* 2 mm for *c–e;* 1 mm for *f–h,j,k;* 0.5 mm for *i,l–o.*)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Capsules substipitate (Figure 54*j*), obovate to obovate-elliptic, dehiscent, bivalved, trilocular, 3.6–4.3(–5) mm long, 1.95–2.1(–2.55) mm wide, tan with dark brown spots, lustrous, puberulous, apex emarginate, dorsal valve (Figure 54*k*) deciduous, dorsal locule very prominent, 1-seeded (or occasionally empty), ventral locules each 2-(or, by abortion, 1-)seeded, cells of the capsule wall transversely elongate. Dorsal locule seed (Figure 54*l,m;* Plate 6*i*) broadly elliptic, 1.65–2.15 mm long, 1.35–1.55 mm wide, ~1 mm thick, hilum dark brown, arising from a very shallow groove, much shorter than the seed, testa orange-buff, heavily spotted and striped with dark brown (or maroon?), nearly smooth on the dorsal surface, not at all white-farinose to sparsely so around the embryotega and hilum, hypha-like filaments absent. Ventral locule seeds (Figure 54*n,o;* Plate 6*i*) ovate to subtriangular (sometimes somewhat 3-lobed), apical seeds rounded apically, basal seeds angular basally, (1.35–)1.45–1.7(–1.8) mm long, 1.4–1.75 mm wide, 0.9–1.2 mm thick, hilum dark brown, prominently raised within a groove, ± not extended onto apical and basal surfaces, testa tan, orange-buff or orange-brown, usually heavily spotted and striped with dark brown (or maroon?), shallowly scrobiculate or sulcate-scrobiculate on the dorsal surface, sparsely white-farinose in many of the depressions, densely so around the embryotega and hilum, hypha-like filaments sometimes present among the farinose granules.

HABITAT.—Coastal sand dunes; ~0–50 m.

FLOWERING.—Flowering specimens have been seen from July and August. In the field the flowers open 0900–0930 hrs and fade ~1300 hrs.

CHROMOSOME NUMBER.—$2n = 26$.

DISTRIBUTION.—N Kenya coast (Map 16).

SPECIMENS SEEN.—KENYA. LAMU: Kitwa Pembe Hill and vicinity, 2°27′S, 40°42′E, *Faden & Faden 74/1083* (BR, C, EA, FT, K, MO, PRE, US, UPS); Lamu Island, *Schlieben 12121* (K).

DISCUSSION

Schlieben's plants differ from the Fadens' in having shorter internodes and apparently somewhat fleshy leaves. They were probably growing more exposed to the effects of salt-laden sea breezes than were the Fadens' plants which came from the sheltered, leeward side of 45–60 m high sand dunes.

Plants of *A. lamuense* show great variation in habit, ranging from unbranched, erect individuals a few centimeters tall to much-branched ones up to about 40 cm tall and 50 cm in diameter. In general, the shoots are erect to ascending; only in the largest plants do they become somewhat decumbent.

The inflorescences have the same basic structure as those of *A. clarkei* and *A. succulentum* (Figure 9). Unlike either of these species, those of *A. lamuense* are nearly all sessile or subsessile. They show the same tendency as *A. clarkei* for the terminal inflorescence of the larger flowering shoots to become associated with the subterminal inflorescence-shoot (see discussion under *A. clarkei*). In *A. lamuense,* secondary inflorescences are often also produced in the axils of the inflorescence bracts of these two inflorescences. This can make interpretation of the inflorescence structure very difficult, as under these circumstances, 11 bracts (four inflorescence bracts, four cincinnus bracts, and three prophylls) plus a foliage leaf are present in addition to the four cincinni. The production of numerous inflorescences in *A. lamuense* (as compared with *A. clarkei* and *A. succulentum*) is consistent with its annual habit that places a high premium on seed production.

The stamen retention mechanism is poorly developed in *A. lamuense*. In the field the period for which the lateral stamens were held by the medial petal could not be determined because visiting bees appeared to be instrumental in their early release. However, in cultivation the stamens were found to be released in less than an hour and often after only a few minutes, suggesting that the pollinators were not the cause of the early release. The anthers escape from a very narrow gap between the still involute, lateral margins of the medial petal.

Aneilema lamuense is highly distinctive because of its inflorescence structure and fruiting pedicel curvature, characters it shares only with *A. clarkei* and *A. succulentum,* its closest relatives. *Aneilema lamuense* differs from the former by its smaller flowers and narrower capsules, from the latter by its petiolate leaves and larger capsules and seeds, and from both by its annual habit, long, uniseriate hairs on the pedicels and lateral sepals, petal color, staminode lobes with pinkish purple or violet spots at their bases, and white medial anther with white pollen. It is also ecologically distinct from both.

12. *Aneilema succulentum* Faden, new species

Herbae perennes internodiis succulentis foliis succulentis distichis laminis sessilibus anguste lanceolato-ellipticis vel ellipticis, (1.3–)1.5–4 (–6) cm longis, (0.4–)0.7–1.3(–1.9) cm latis. Inflorescentiae terminales in caulibus floriferis etiam in caulibus brevibus e nodis 1–4 summis caulium floriferorum prodientibus, cincinnis brevibus solitariis jugo bractearum subtentis et partim inclusis compositae. Pedicelli 7–10(–13) mm longi, in fructu valde recurvati (~180°) tantum prope apicem. Petalum medium cymbiforme vel cupulatum. Filamenta stamineum et staminodiorum basi connata. Capsulae (2.8–)3.2–3.7(–4.3) mm longae, (1.5–)2.1–2.3(–2.5) mm latae valva dorsali saepe decidua, loculo dorsali 1-seminali, loculis ventralibus uterque 2-seminalibus. Semina loculorum ventralium subtriangularis vel ovata, 1.3–1.5(–1.6) mm longa, 1.3–1.5 mm lata, testa scrobiculata non profunda (Figure 55).

TYPE.—Kenya, Tana River District [Lamu District on label], Garsen–Witu road, near Nyangoro Bridge, 2°18′S, 40°20′E, 20–21 Jul 1974, *Faden & Faden 74/1152* (US, holotype; BR, EA,FT, K, MO, PRE, isotypes).

Perennial herbs (habit type IIA2, Figures 2, 55*a*). Roots

fibrous. Vegetative shoots repent, sometimes with looping internodes, much branched, often forming mats; flowering shoots ascending, unbranched or little branched, to ~15–30 cm tall. Internodes (0.5–)1–5(–8) cm long, often suffused with maroon, puberulous, very succulent, circular to semicircular or elliptic in transverse section, becoming swollen in the rainy season, the nodes then appearing as constrictions. Leaves distichous (the 2 ranks at acute or right angles to each other), usually not reduced apically on the flowering shoots, sheaths 2–6(–10) mm long, pilose-puberulous, ciliate at the apex, laminae succulent, often slightly falcate, often somewhat conduplicate, sessile, narrowly lanceolate-elliptic to elliptic (rarely ovate-elliptic), (1.3–)1.5–4(–6) cm long, (0.4–)0.7–1.3(–1.9) cm wide, apex acute, base slightly asymmetric, cuneate, margin planar or undulate, scabrid, sparsely ciliate towards the base, often maroon, both surfaces slightly lustrous, adaxial frequently mottled with maroon, puberulous or pilose-puberulous, abaxial pilose-puberulous, the uniseriate hairs generally shorter (occasionally equal to) and more numerous than those of the adaxial surface.

Inflorescences (Figure 55*b;* Plate 4*e*) terminal on the flowering shoots and also on short, non-perforating shoots produced from the uppermost 1–4 nodes on the flowering shoots, sometimes longer lateral shoots, produced from the lower nodes of the main flowering shoot, also bearing 1 or 2 inflorescences in the same manner as the main flowering shoot; each inflorescence consisting of a short, solitary cincinnus subtended by, and partially enclosed in, a subopposite pair of herbaceous (at least at their apices) bracts, the larger, lower one the inflorescence bract, the upper the cincinnus bract. Peduncles ~0–4 cm long (to 7 cm long in cultivation), green, puberulous. Inflorescence bract terminal, herbaceous, slightly falcate. Cincinni to ~5 mm long and 10-flowered (to 7 mm long and 20-flowered in cultivation). Cincinnus bracts completely membranous or herbaceous apically and membranous basally, linear-lanceolate to lanceolate, falcate, erect to ascending, 10–22 mm long (including the sheath), 1.5–5 mm wide, eglandular, densely pilose-puberulous on the adaxial surface, puberulous (occasionally sparsely pilose as well) on the abaxial surface, margin ciliate. Cincinnus peduncles not developed. Cincinnus axes very short, completely covered by overlapping bracteoles, glabrous. Bracteoles attached up to 0.2 mm apart, membranous, strongly eccentrically cup-shaped, perfoliate, 3.25–7 mm long, 1–3 mm high, slightly thickened apically but apparently eglandular, sparsely puberulous apically with uniseriate hairs and/or hook-hairs, rarely glabrous.

Flowers perfect and staminate, odorless, 9–14(–17) mm wide (Figure 55*c,d;* Plate 4*f*). Pedicels 7–10(–13) mm long, arcuate-erect to gently S-shaped in flower, in fruit, strongly recurved (~180°) only near the apex and becoming much thickened in that region (Figure 55*j*), persistent, puberulous near the apex, otherwise glabrous. Sepals inconspicuously glandular or apparently eglandular near the apex (glands, when present, unlobed) glabrous, or puberulous basally; medial sepal lanceolate to lanceolate-elliptic, 3.5–4(–4.5) mm long, 1.8–2.3 mm wide; lateral sepals elliptic to ovate, 4–4.5(–5.5) mm long, 2.5–3.2 mm wide. Paired petals 7–8(–10.5) mm long, 5–7(–9) mm wide (Figure 55*e*), limb ovate-elliptic to ovate or reniform, 4.5–5.5(–7) mm long, white to pale lilac (RHS colors (those too pale to be measured omitted): 76C, *Faden et al. 70/937* and *72/39,* both cultivated; 76C-D, *Evans & Maikweki 54,* cultivated, *Faden & Faden 74/1152* and *74/1186,* both field & cultivated; 76D, *Faden & Faden 74/1152,* cultivated), apex subacute to obtuse or rounded, claw 1.5–2.5 (–3.5) mm long, white or whitish, glabrous. Medial petal boat-or cup-shaped, sometimes ± carinate medially, ovate to obovate, broadest at the margin (viewed from the apex), which is generally slightly revolute towards the apex, frequently retaining the lateral stamens when the flower opens, 5.5–7 (–9.5) mm long, 3–5(–7) mm wide, (2–)2.5–3(–5) mm deep, concolorous with the limbs of the paired petals when they are whitish, distinctly paler than the latter when they are pale lilac (Figure 24*g–i*). Lateral stamen filaments fused basally to medial stamen filament and lateral staminode filaments (Figures 28*b,* 55*h*), stamen filaments shortly adnate to the medial petal base. Medial staminode filament 0.5–2 mm long, white or greenish, often shading to yellow at the apex, antherode bilobed, lobes sessile, ovate, obovate, reniform, lanceolate or transversely elliptic, 0.15–0.4 mm long, connective not at all to slightly elongate (Figure 55*f*). Lateral staminodes with filaments 3–4(–5) mm long, ventrally displaced, white or whitish, shading to yellow apically, antherodes bilobed, yellow, lobes sessile to shortly stipitate, obovate-cuneate to transversely elliptic or subreniform, 0.4–0.9 mm long, connective slightly to not at all elongate (Figure 55*g*). Lateral stamens with filaments parallel to slightly divergent, sometimes (always?) slightly longer and more divergent in staminate than in perfect flowers (Figures 28*b,* 55*h*), 5–6(–7) mm long, S-shaped, arcuate-decurved or sharply geniculate near the middle, anthers ovate to elliptic or lanceolate-elliptic, (0.7–)0.9–1.4 mm long, (0.45–)0.6–1 mm wide, pollen white or, less commonly, orange-yellow. Medial stamen with filament 4–5(–5.5) mm long, anther lanceolate to ovate or ovate-elliptic, saddle-shaped, (1.2–)1.5–2.3 mm long, 1–1.2 mm wide, pollen orange-yellow. Ovary substipitate to shortly stipitate (Figure 55*i*), obovate to obovate-oblong or obovate-elliptic, 1.3–1.6 mm long (including the stalk or cuneate base), 0.9–1.1 mm wide, densely and uniformly covered with patent, glandular hairs, rarely mixed with 1 (or more?) hook-hair(s), apex rounded to truncate, dorsal locule prominent, 1-ovulate, ventral locules each 2-ovulate; style 5.5–7 mm long, very gently arcuate-decurved, usually held slightly out of the floral midplane, sometimes with a few glandular hairs towards the base, stigma capitate, held in front of the anthers and slightly above to slightly below them.

Capsules (Figure 55*j*) substipitate to shortly stipitate, elliptic to obovate-elliptic, carinate midventrally, dehiscent, bivalved, trilocular, (2.8–)3.2–3.7(–4.3) mm long, (1.5–)2.1–2.3(–2.5)

mm wide, grayish tan, frequently with small, dark brown spots or mottling, lustrous, puberulous, apex truncate to emarginate, dorsal valve (Figure 55*k*) frequently deciduous, dorsal locule prominent, 1-seeded (rarely empty), ventral locules each 2-(or, by abortion, 1-) seeded, cells of the capsule wall transversely elongate. Seeds (Figure 55*l–o;* Plate 6*j*) broadly elliptic to broadly ovate, 1.35–1.55 mm long, 1.2–1.25 mm wide (dorsal locule seed) or subtriangular to ovate (sometimes somewhat 3-lobed), with apical seeds rounded apically and basal seeds angular basally, 1.3–1.5(–1.6) mm long, 1.3–1.5 mm wide (ventral locule seeds), 0.8–1 mm thick, hilum dark brown, prominently raised within a groove, not extended onto apical and basal surfaces, testa tan or grayish tan, sometimes marked with brown spots and streaks, shallowly scrobiculate (the pits sometimes distinctly elongate), white-farinose around the embryotega and hilum and frequently sparsely so in some of the depressions, hypha-like filaments sometimes present among the farinose granules.

HABITAT.—Dry deciduous bushland and bushland thicket dominated by species of *Commiphora, Euphorbia, Lannea, Boswellia, Combretum, Grewia, Sansevieria,* or, less commonly, *Diospyros* or *Acacia;* also in *Brachystegia* forest or woodland and along roadsides; sandy or clayey soils, occasionally on rocks; usually in partial shade or full sun; ~10–600 m.

FLOWERING.—Flowering specimens have been seen from January, April, May, July, October, and December. In the field the flowers open 1130–1230 hrs and fade 1445–1530 hrs (Figure 25).

CHROMOSOME NUMBER.—$n = 13$, $2n = 26$.

DISTRIBUTION.—E Kenya (might be expected in NE Tanzania) (Map 16).

SPECIMENS SEEN.—KENYA. KILIFI: Kaloleni–Mariakani road, *Evans & Maikweki 54,* cultivated in Nairobi (EA); Sala Gate–Malindi road, 7 km towards Sala Gate from junction with Bamba–Kakoneni road, ~3°11′S, 39°45′E, *Faden & Faden 72/30* (EA, K, MO); Kakoneni–Jilore Forest Station road km 2.5, 3°11′S, 39°52.5′E, *Faden et al. 72/39* (EA, K, MO, P, US, WAG); Malindi, *Rawlins 863* (EA, K). KWALE: Near Taru, Samburu–Mackinnon Road, km 8, *Faden & Evans 70/782* (EA, K, MO); 1 km S of Taru on Mombasa–Nairobi road, 3°46′S, 39°07′E, *Faden & Faden 72/91* (EA, K); Nairobi–Mombasa road, 5.3 km towards Mombasa from Taru, ~3°46′S, 39°10′E, *Faden & Faden 74/1281* (DSM, EA, K, MO); Mombasa–Nairobi road, 2.5 km towards Mombasa from turnoff to Maji ya Chumvi Railway Station, 3°49′S, 39°20′E, *Faden & Faden 77/574* (EA, F, US); Mackinnon Road–Samburu, 19.4 km, *Faden et al. 70/937* (B, EA, FT, K, MO, US, UPS); Taru Desert, Taru, *Tweedie 1202* (K). TANA RIVER: Garsen–Witu road, near Nyangoro Bridge, 2°18′S, 40°20′E, *Faden & Faden 74/1152* (BR, EA, FT, K, MO, PRE, US); Garsen–Malindi road, 1.5 km towards Malindi from turnoff to Oda, 2°32′S, 40°07′30″E, *Faden & Faden 74/1186* (C, EA, K, MO, US, WAG); Garsen–Malindi road, ~8 km from Garsen, ~2°22′S, 40°07′E, *Faden et al. 72/227* (EA, K); Kurawa, 30 mi S of Garsen, *Polhill & Paulo 629* (BR, EA, K, PRE); Lamu area, Malango ya Simba Forest, *Rawlins 454* (EA, K). TEITA: Mackinnon Road–Bachuma, 9.6 km, 3°40′S, 38°58′E, *Faden & Evans 71/620* (BR, EA, K); Nairobi–Mombasa road, 11.7 km towards Mombasa past Maungu Station, ~3°37′S, 38°50′E, *Faden & Faden 74/524* (EA, K, MO, US); Mt. Kasigau, lower slopes of S side above Bungule, *Faden et al. 70/969* (EA); Taru desert near Maungu, *Tweedie 3364* (K).

DISCUSSION

Aneilema succulentum is one of the most succulent species in the genus, although much less so than some other Commelinaceae. In the dry season the thick internodes become laterally compressed due to the loss of water. The leaves also store water, particularly in the vertically elongate cells of the upper epidermis. In this character and in their general fleshiness they resemble the leaves of *A. zebrinum.*

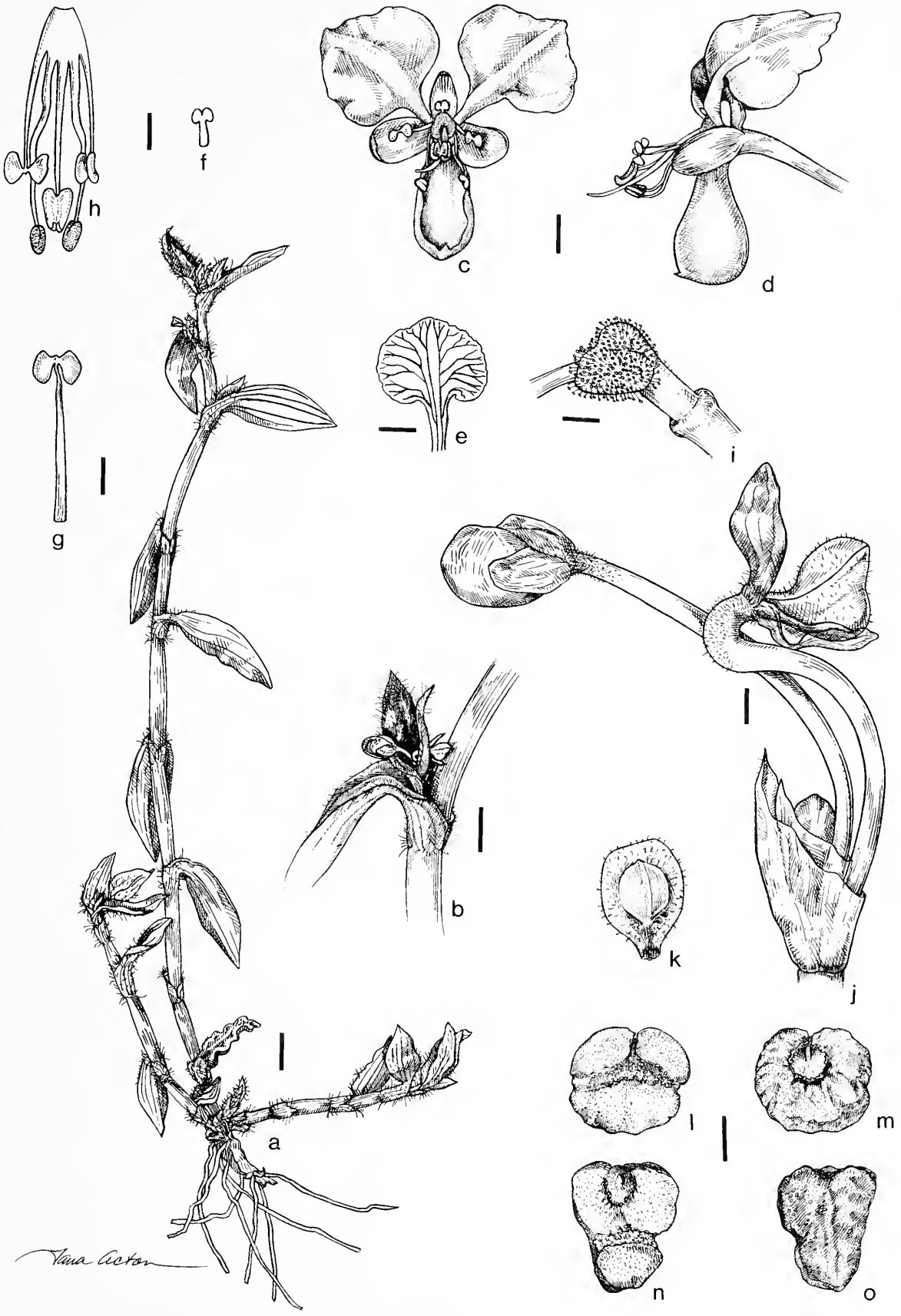
The inflorescences are identical in structure to those of *A. clarkei* and *A. lamuense* (see discussion under the former and Figure 9). The flowering shoots of *A. succulentum* tend to be more branched and therefore to produce more inflorescences than those of *A. clarkei.* In addition, the last two inflorescences on a flowering shoot show very little tendency to become paired as frequently happens in both *A. clarkei* and *A. lamuense.*

The flowers of *A. succulentum* are considerably larger in cultivation (under a daily watering regimen) than in the field. The greatest dimensions for various floral parts given above (usually in parentheses) are mostly from flowers in cultivation. The normal range is taken from field collected flowers.

The presence or absence of subapical glands on the sepals is not always readily determinable. In some populations they are clearly present on all three sepals. In others they appear to be lacking on the lateral sepals and perhaps also on the medial. The distinct absence of glands from the lateral sepals in the latter case can be observed in flowers preserved in FAA, which acts as a partial clearing agent for sepals. Anatomical studies are needed to determine more precisely what constitutes "presence" or "absence" of glands.

The stamen retention mechanism of the medial petal is poorly developed in *A. succulentum.* It has been noted both in field populations and cultivated plants that frequently some flowers have one or both stamens free when the flowers open.

FIGURE 55.—*Aneilema succulentum* Faden, new species: *a,* habit; *b,* axillary inflorescence; *c,* perfect flower, front view; *d,* perfect flower, side view; *e,* paired petal; *f,* medial staminode; *g,* lateral staminode; *h,* androecium of perfect flower, top view, medial staminode omitted, gynoecium removed; *i,* ovary and base of style, side view; *j,* mature bud and capsule attached to cincinnus, side view; *k,* dorsal capsule valve, dorsal view; *l,* dorsal locule seed, ventral view; *m,* dorsal locule seed, dorsal view; *n,* ventral locule seed, ventral view; *o,* ventral locule seed, dorsal view (all from *Faden & Faden 74/1152*). (Bars = 10 mm for *a;* 4 mm for *b;* 2 mm for *c–e;* 1 mm for *f-h,j,k;* 0.5 mm for *i,l–o.*)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Furthermore, in no case are the stamens held for more than half an hour (Figure 25).

Pollen grains of the lateral anthers may be white or orange-yellow. In the latter case they are concolorous with the pollen of the medial anther. White appears to be the common (or exclusive?) color of lateral anther pollen observed in the field. Orange-yellow pollen is common in cultivated plants (including those observed in the field to have white pollen). The possibility of the orange-yellow color being an artifact of cultivation needs further investigation.

The occurrence of *A. succulentum* in *Brachystegia* woodland in the Kilifi District is interesting, because the closely related *A. clarkei* also frequently grows under *Brachystegia* in the same district. However, the soils and understory shrubs and herbs are quite different where each of the two occurs. Most notable is the presence of numerous succulents—e.g., *Euphorbia grandicornis* (= *breviarticulata*) is the dominant understory shrub—in those *Brachystegia* habitats where *A. succulentum* is present. Succulents are completely lacking in the *Brachystegia* woodland containing *A. clarkei*. The two species have not been found together.

In the inland localities (Teita and Kwale districts) and in Kilifi District, *A. succulentum* occurs only in sandy soil or occasionally in well-drained rocky habitats. In Tana River District it grows mostly on a clayey alluvium mixed with sand.

Aneilema succulentum appears to have two flowering periods inland, April to June and October to December or January, corresponding to the two rainy seasons in this region. In the Tana River District it may have one long flowering season (April to November?) or perhaps two.

Sterile plants of *A. succulentum* can readily be confused with *A. zebrinum*, and the two have been found growing together near Taru and not far from one one another on Mt. Kasigau. *Aneilema succulentum* can be distinguished by its thicker internodes, proportionally narrower leaves with asymmetric bases, and the two ranks of leaves at acute or right angles to one other.

Aneilema succulentum is distinctive because of its vegetative and inflorescence morphology and fruiting pedicel curvature. The latter two characters are otherwise known only in *A. clarkei* and *A. lamuense*. It differs from the former by its smaller flowers, from the latter by its perennial habit, and from both by its more succulent internodes, the two ranks of leaves arranged at acute or right angles to each other, more succulent and sessile leaves with asymmetric bases, color of the paired petals, general lack of hook-hairs on the ovaries and capsules, and smaller capsules and seeds.

13. *Aneilema zebrinum* Chiovenda

Aneilema zebrinum Chiovenda ["zebrina"], Webbia, 8:38, fig. 12, p. 39, 1951.—Obermeyer and Faden in Leistner, Fl. Southern Africa, 4(2):40, figs. 8, 9-3a,b, 1985. [Syntypes: Ethiopia, Gemu-Gofa Prov., rive del Caschei, 5 Jul 1939, *Corradi 2154* (FT; photo K); same locality, 4 Jul 1939, *Corradi 2163* (FT; photo K); Cashei, 6 Jul 1939, *Corradi 2155* (FT, photo K: lectotype of Brenan, Kew Bull., 19:67, 1964).]

Ballya zebrina (Chiovenda) Brenan, Kew Bull., 19:64, map 1, p. 65, fig. 1, p. 66, 1964.—Cufodontis, Bull. Jard. Bot. Natl. Belgique, 41, suppl., 1519, 1971.—Ross, F. Natal, 117, 1972.—Faden in Agnew, Upland Kenya Wild Fl., 653, 1974.

Perennial herbs (habit type IIb, Figure 2). Roots fibrous. Shoots repent, sparsely branched (usually unbranched for some distance behind the shoot apex) (Plate 4*g*). Internodes slender, (0.6–)1–3(–4) cm long, puberulous. Leaves distichous (the 2 ranks usually at an obtuse, or rarely acute, angle to each other), sheaths 3–9 mm long, puberulous and usually sparsely pilose, ciliate at the apex, laminae somewhat succulent, sessile, ovate to ovate-elliptic or occasionally elliptic, 1–3.5(–4) cm long, 0.5–2 cm wide, apex acute or occasionally obtuse, thickened and usually mucronate, base symmetric, usually amplexicaul, margin usually planar, ciliolate, scabrid in dried specimens but not in life, sparsely ciliate towards the base, both surfaces lustrous, puberulous with a mixture of equal-sized hook-hairs and uniseriate hairs, adaxial surface with very pale veins, often mottled with maroon between the veins when not so mottled, often gray-green (Plate 4*g*).

Inflorescences axillary, perforating the leaf sheaths (Plate 4*h*), generally consisting of one (rarely 2), short cincinnus subtended by 3 bracts, the basal a prophyll, the middle the inflorescence bract, the apical the cincinnus bract, frequently a secondary inflorescence, consisting of a single cincinnus with 2 or 3 bracts at its base, developing from the axil of the inflorescence bract, rarely another secondary inflorescence, consisting of one cincinnus, developing from a prophyllar bud. Peduncles up to 8 mm long (often not developed), puberulous. Inflorescence bract basal to apical, bract-like, membranous. Inflorescence axis puberulous. Cincinni to ~2 cm long and 4(–6)-flowered. Cincinnus bracts erect to ascending, membranous, lanceolate to ovate, ~2–3.5 mm long, eglandular, puberulous with ciliate or ciliolate margins. Cincinnus peduncles 1–5(–8) mm long, puberulous. Cincinnus axes puberulous. Bracteoles attached 0.5–2(–4.5) mm apart, membranous, eccentrically cup-shaped, perfoliate, 1.2–2(–2.2) mm long, 0.3–1 mm high, eglandular, densely puberulous with hook-hairs and uniseriate hairs.

Flowers perfect and (very rarely) staminate, odorless, 7–10 mm wide (Plate 4*h*). Pedicels (0.5–)1.5–3.5 mm long (to 5 mm long in fruit), ascending to erect in flower, erect to slightly further recurved in fruit, puberulous. Sepals apparently eglandular, puberulous with a mixture of hook-hairs and uniseriate hairs, the latter sometimes absent from the lateral sepals; medial sepal ovate-elliptic to lanceolate-elliptic or ovate, 2–2.7 mm long, (1–)1.5–1.6 mm wide; lateral sepals ovate-elliptic to elliptic or oblong-elliptic, 2.3–3 mm long, 1.5–1.9 mm wide. Paired petals held in a lateral position, 4–5.7 mm long, 3.1–4.5 mm wide, limb ovate to broadly ovate, 2.5–3.7 mm long, pale lilac (RHS colors: 75B, *Faden & Faden 74/482*; 76B-C, same collection, cultivated, *Faden & Faden*

74/1052; 76C, *Faden et al. 74/205*, *Faden et al. 74/330*, cultivated, *Faden & Faden 74/533*), apex rounded, margin ± entire, claw 1.25–2 mm long, whitish, glabrous. Medial petal cup-shaped, ovate, broadest at or near the margin (viewed from the apex), not retaining the stamens when the flower opens, 3.5–4.7 mm long, 2.7–4 mm wide, 1.7–2 mm deep, concolorous with the limbs of the paired petals (Figure 24*j–l*). Lateral stamen filaments fused basally to medial stamen filament and to the lateral staminode filaments, medial staminode nearly free (Figure 27*c*). Medial staminode usually completely hidden within the medial sepal, filament (1–)1.5–1.8 mm long, white, shading to yellow at the apex, antherode bilobed, yellow, lobes sessile, obovate-cuneate to suborbicular or transversely elliptic, 0.15–0.3 mm long, connective not elongate. Lateral staminodes with filaments (2–)2.2–2.6 (–3.5) mm long, displaced ventrally, white to very pale lilac, shading to yellow at the apex, antherode bilobed (or occasionally unlobed and clavate), yellow, lobes sessile, ovobate-cuneate, 0.1–0.4 mm long, connective not elongate. Lateral stamens nearly parallel for their entire length or, more commonly, parallel or divergent from the fused portion to above the middle, then convergent apically, 3–3.5(–4.5) mm long, ± S-shaped, decurved above the middle, glabrous, anthers often in contact with each other and with the medial anther, ovate to broadly ovate, 0.5–0.55 mm long, 0.45–0.6 mm wide, pollen yellow. Medial stamen with filament 2.5–2.8(–3.6) mm long, anther ovate to broadly ovate or ovate-quadrate, slightly saddle-shaped, 0.6–0.85 mm long, 0.6–0.8 mm wide, pollen yellow. Ovary substipitate, obovate to obovate-elliptic, (1–)1.2–1.5 mm long, (0.75–)0.9–1 mm wide, densely and uniformly covered with a mixture of glandular hairs and hook-hairs (the latter generally more numerous) (Figure 42*l,m*), rarely mixed with a few uniseriate hairs, apex rounded, dorsal locule 1-ovulate, ventral locules each 2-ovulate, style 2.7–3.2 (–3.6) mm long, arcuate-decurved for most of its length, held in the floral midplane or slightly curved laterally out of it, stigma capitate, often touching the anthers, but sometimes well below them.

Capsules substipitate, obovate-elliptic, indehiscent or partially dehiscent along the lateral sutures, beginning at the base, bivalved (when partially dehiscent), trilocular, 3–4 mm long, 2.1–2.5(–3) mm wide, stramineus or rarely chocolate brown, lustrous, puberulous, apex obtuse to rounded or truncate, valves persistent, dorsal locule a low hump, 1-seeded (or occasionally empty), ventral locules each 2-(or, by abortion, 1-)seeded, cells of the capsule wall transversely elongate. Seeds (Plate 7*a*) broadly elliptic to reniform, 1.4–1.8 mm long, 1.05–1.25 mm wide (dorsal locule seed), or ovate to ovate-cordate, with apical seed rounded apically and basal seed rounded or angular basally, 1.25–1.6 mm long, (1.1–)1.2–1.5 mm wide (ventral locule seeds), 0.5–0.6 mm thick, hilum slate gray or black, in a very shallow groove or not in a groove, not extended onto apical or basal surfaces, testa gray or grayish brown, shallowly reticulate on the dorsal surface, sparsely tan-farinose around the embryotega and occasionally around the hilum, or occasionally farinose granules completely lacking.

HABITAT.—Deciduous or semi-evergreen bushland and bushland thickets often dominated by species of *Acacia* and/or *Commiphora*, also in woodland, woodland thickets and light forest, sometimes in rocky areas, occasionally on steep slopes; sandy or clayey soils; partial or dense shade; 10–1150 m.

FLOWERING.—Flowering specimens have been seen from January, February, April, May, July, and December. In the field the flowers open 1030–1115 hrs and fade 1315–1430 hrs.

CHROMOSOME NUMBER.—$n = 13$, $2n = 26$.

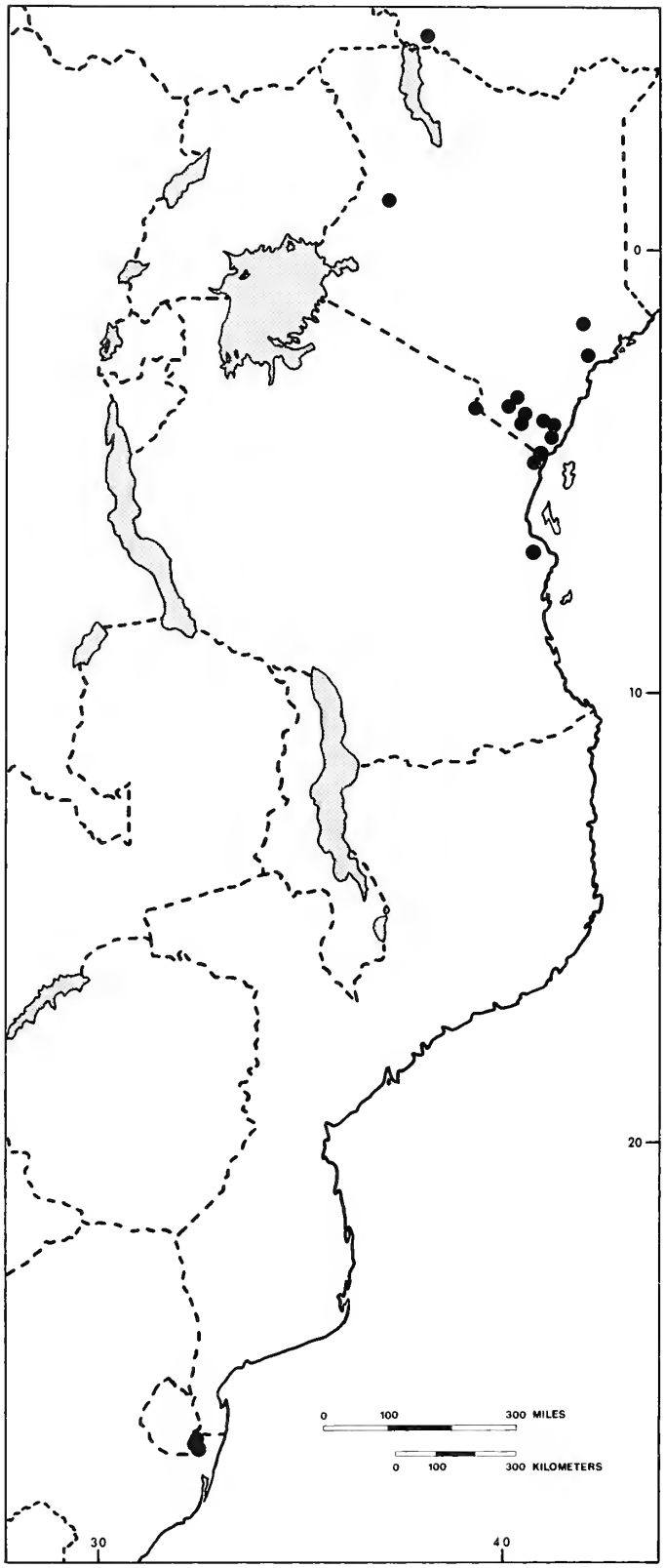
DISTRIBUTION.—SW Ethiopia to Tanzania, also in South Africa (N Natal) (Map 17).

SPECIMENS SEEN.—ETHIOPIA. GEMU-GOFA: Rive del Caschei, *Corradi 2154* (FT; photo K) & *2163* (FT; photo K); Caschei, *Corradi 2155* (FT; photo K).

KENYA. ELGEYO: Kerio Valley, Tot, *Bally B12348* (K); 2.1 km S of Tot, *Faden et al. 70/888* (EA, K, US, WAG). KWALE: Tanga–Mombasa road, mi 36, *Bally B12193* (K); Mombasa–Nairobi road, mi 30, *Bally B13931* (EA, G); near Maji ya Chumvi, between Samburu and Mariakani, *Bally & Smith B14320* (K); ~1 km S of Taru on Mombasa–Nairobi road, 3°46′S, 39°07′E, *Faden & Faden 72/92* (BR, EA, K, MO, US); 5.3 km towards Mombasa from Taru on Nairobi–Mombasa road, ~3°46′S, 39°10′E, *Faden & Faden 74/1283* (EA, FT, K, MO, US); Lungalunga–Vanga road, ~0.5 km, 4°33′S, 35°07′30″E, *Faden & Faden 77/364* (EA, F, K, US, WAG); Mombasa–Nairobi road, 2.5 km towards Mombasa from turnoff to Maji ya Chumvi Railway Station, 3°49′S, 39°20′E, *Faden & Faden 77/585* (EA, F, US). TANA RIVER: 13 km from Galole on Galole–Garsen road, ~1°37′S, 39°59E′, *Faden & Faden 74/1052* (BR, C, EA, FT, K, MO, PRE, UPS, US); 0.8 km towards Garsen from turnoff to Kibusu on Malindi–Garsen road, 2°21′S, 40°07′E, *Faden & Faden 74/1176* (EA, K, MO, US). TEITA: 28 km on Voi–Taveta road from Nairobi–Mombasa road turnoff, 3°30′S, 38°19′E, *Faden & Faden 74/482* (MO); 18 km on Voi–Taveta road from Nairobi–Mombasa road turnoff, ~3°30′S, 38°24′E, *Faden & Faden 74/533* (B, EA, K, MO, US); same locality, *Faden & Faden 77/311* (EA, F, US); Maungu Hills, 3°38′S, 38°45′E, *Faden et al. 70/183* (EA, K); Mt. Kasigau, lower slopes of S side above Bungule, *Faden et al. 70/966* (EA, K, MO); Mzinga Hill, Voi, *Verdcourt 3892* (EA, K).

TANZANIA. BAGAMOYO: Dar es Salaam–Morogoro road, ~10 km E of Chalinze (~85 km W of Dar), *Mhoro & Wingfield BM2411* (EA). PARE: Between N Pare Hill & N end of Lake Jipe, *Bally B12145* (K; also cultivated at K). TANGA: 3 km towards Maramba from turnoff to Lelwa on Maramba (Malamba)–Korogwe road, 4°46′S, 38°47′E, *Faden et al. 74/330* (DSM, EA, K, MO, US).

SOUTH AFRICA. NATAL: 2632 (Bela Vista): Ndumu Game Reserve, Mahemane Thicket, ~26°53′S, 32°15′E (-CD), *Faden et al. 74/205* (BOL, EA, K, MO, NH, NU, PRE, US); Ndumu Game Reserve, E of Shokwe (-CD), *Poole 1255* (K, MO). 2732



MAP 17.—Distribution of *Aneilema zebrinum* Chiovenda.

(Ubombo): Mkuzi flats E of Jozini (-AC), *Brenan 14243* (K); Sandforest (-AD), *Strey 4752* (PRE).

DISCUSSION

Corradi 2155 was selected as the lectotype of this species by Brenan (1964), whose choice must be followed (*International Code of Botanical Nomenclature,* Article 8, 1983). This was clearly the best choice, as it is the sheet illustrated in the figure accompanying the type description. The selection of *Corradi 2154* by Cufodontis (1971) as the lectotype should be ignored.

The monospecific genus *Ballya,* based on *A. zebrinum,* was distinguished from *Aneilema* by Brenan (1964) primarily on the basis of three characters: (1) *Ballya* flowers having an inverted symmetry of *Aneilema* flowers, i.e, medial petal uppermost, staminodes lowermost, etc., (2) *Ballya* inflorescences perforating the leaf sheaths vs. not perforating in *Aneilema,* and (3) *Ballya* stamen and lateral staminode filaments being fused basally vs. free in *Aneilema.* Of these characters the first has been found to be atypical of *A. zebrinum* itself. Its flowers usually have the same orientation as those of *Aneilema,* or at least not an inverted one. This has been observed in the field in a number of populations as well as in cultivation. The flowers in Brenan's plant were inverted because the plant was cultivated as a hanging basket, and its unusually short pedicels prevented reorientation of the flowers to a more normal position. Such reorientation has been observed to occur in other species of *Aneilema* and even in other populations of *A. zebrinum* with longer pedicels.

The remaining two characters, supposedly unique to *Ballya,* also occur in species of *Aneilema.* The stamen filament bases are fused in all species of section *Lamprodithyros* as well as in *A. hockii* of section *Amelina.* Most of these species also have the lateral staminode filaments at least shortly fused basally to the stamens, as in *A. zebrinum.* Perforating inflorescences occur in *A. petersii* subsp. *pallidiflorum* and *A. tanaense* (both section *Lamprodithyros*), although no *Aneilema* species produces them almost exclusively except *A. zebrinum.* A single terminal inflorescence noted on a long shoot of this species is further evidence of its basic similarity to other *Aneilema* species.

Tomlinson (1966:387) used anatomical data to try to separate *Ballya* from *Aneilema.* He stated that *Ballya* differed from *Aneilema* by the former's glandular microhairs having an indistinct basal septum and the distal cell usually being longer than the middle cell, in contrast to the basal septum "obvious" and the "distal [cell] often shorter than [the] middle cell" in *Aneilema.* He further distinguished *A. zebrinum* by its epidermal cells vertically elongate in transverse section, whereas those of other *Aneilema* species were not elongate.

Tomlinson's conclusions were based on a sample of *Aneilema* species that was small and unrepresentative of the genus as a whole. The seven or eight species he examined (listed in Tomlinson, 1969) did not include any of section *Lamprodithyros.* The present study does not support Tomlin-

son's conclusion about the distinctions between *Ballya* and *Aneilema*. The glandular microhairs of *A. zebrinum* have been found to usually have the distal cell shorter than the middle cell (see Tomlinson, 1966, figs. 6, 114), a character that is found in a number of *Aneilema* species, including *A. succulentum* (section *Lamprodithyros*). The distinctness of the basal septum is open to subjective interpretation. I could find no difference in this character between *A. zebrinum* and *A. succulentum*. The latter species also has vertically elongate upper epidermal cells very much like those of *A. zebrinum*. Thus *Ballya* is not distinct from *Aneilema*.

The flowers of *A. zebrinum* are often borne under the leaves. The small space available for them probably accounts for their being tilted or more or less vertical rather than horizontal as in most other *Aneilema* species. The lateral position of the paired petals may also be the consequence of space constraints. Individual flowers remain open for about three hours. *Aneilema zebrinum* has probably been overlooked by collectors because of its prostrate habit and tendency to grow under shrubs. Even when spotted the plants may be passed over as sterile because of the inconspicuousness of the flowers and capsules. In East Africa there is the further problem that *A. zebrinum* bears a striking resemblance vegetatively to and may occur with *A. succulentum* and an undescribed species of *Cyanotis*. The undercollection of *A. zebrinum* undoubtedly explains the apparent range disjunction of 2400 km between northern Tanzania and South Africa recorded by Faden (1975). The recent report of this species from the Selous Game Reserve in southern Tanzania (Vollesen, 1980) has considerably reduced the gap and and has added evidence that the remaining gap is only an artifact due to the lack of collections.

Aneilema zebrinum exhibits a number of characters that are unusual for the genus as a whole and clearly demonstrate its relationship to species of section *Lamprodithyros*. In addition to the fused filament bases, large, cup-shaped medial petal, perforating inflorescences, and vertically elongate epidermal cells mentioned above, these characters include the repent habit, eglandular bracteoles and sepals, ovary and capsule pubescence frequently composed predominantly of hook-hairs, indehiscent or partially dehiscent capsules, and strongly dorsiventrally compressed seeds.

Although the strictly repent flowering shoots of *A. zebrinum* are unique in *Aneilema*, its mat-forming habit occurs in several species. The particularly strong vegetative similarity to *A. succulentum* has been noted above. As in that species, the primary shoot has spirally arranged leaves. It branches profusely from the lower nodes, producing thereafter only repent shoots with distichous leaves.

The bracteoles in *A. zebrinum* are eglandular, as in *A. clarkei*, *A. lamuense*, and *A. succulentum*, and unlike nearly all other *Aneilema* species. The absence of sepaline glands from *A. zebrinum* suggests an endpoint in the reduction series shown by the same three species: glands are normally present on all sepals in *A. clarkei;* they may be lacking on some or all of the sepals in *A. succulentum;* they are regularly absent from all three sepals in *A. lamuense*. It should be noted that presence or absence of sepaline glands must be used with some caution: sepals with inconspicuous glands may be difficult to distinguish from truly eglandular ones.

The abundance of hook-hairs on the ovaries and capsules of *A. zebrinum*, although very variable, is not matched by any other species in the genus. However, smaller numbers of hook-hairs among more numerous glandular hairs also occur in a number of species of section *Lamprodithyros* (*A. tanaense*, *A. calceolus*, *A. lamuense* (regularly), *A. clarkei* (frequently), and *A. succulentum* and *A. indehiscens* (rarely)). Ovarian hook-hairs have otherwise been noted in *Aneilema* only in *A. gillettii* (section *Amelina*) and very rarely in *A. somaliense* (section *Somaliensia*).

Indehiscent or partially dehiscent capsules and strongly dorsiventrally compressed seeds, present in *A. zebrinum*, also occur together in *A. indehiscens* (section *Lamprodithyros*).

In addition to all of the above characters, several others suggest affinities of *A. zebrinum* with section *Lamprodithyros* and support its placement in that section. Its very reduced inflorescences are homologous to the lateral inflorescence-shoots of *A. clarkei*, *A. lamuense*, and *A. succulentum*. Its five-seeded capsules are common to nearly all species of the section, and its basic chromosome number, $x = 13$, is the same as that of the other species of section *Lamprodithyros*. One may also note that *A. zebrinum*, although very widespread, occurs entirely within the geographic ranges of other species of this section.

Within section *Lamprodithyros*, *A. zebrinum* is most closely related to *A. clarkei*, *A. lamuense*, and *A. succulentum* and especially to the last species. The repent flowering shoots and strictly lateral inflorescences of *A. zebrinum* readily distinguish it from these species.

Section 6: *Brevibarbata* Faden, new section

Herbae perennes vel annuae foliis spiraliter dispositis. Inflorescentiae thyrsi plerumque densi vel modice densi. Bracteolae cupulatae, perfoliatae vel non perfoliatae. Petalum medium deminutum. Filamenta libra. Stamina lateralia filamentis sigmoideis, in dimidio distali subtiliter barbatis. Stamen medium anthera plerumque in magnitudine antheras staminum lateralium subaequanti sed in forma differens. Ovarium glabrum vel puberulum. Capsulae dehiscentes, lucentes, glabrae vel puberulae, valvis persistentibes, loculo dorsali haud evoluto vel 1-seminali, loculis ventralibus uterque 1–3-seminalibus.

TYPE SPECIES.—*Aneilema beniniense* (P. de Beauvois) Kunth.

Perennial or annual herbs with fibrous or tuberous roots. Leaves spirally arranged.

Inflorescences thyrses, terminal and occasionally axillary from the inflorescence bract and upper leaves, usually dense or

moderately dense. Inflorescence bract herbaceous or membranous, when membranous, commonly enclosing the young inflorescence. Inflorescence axis puberulous (rarely subglabrous) with hook-hairs of uniform length or of two sizes (rarely some long, uniseriate hairs also present). Bracteoles cup-shaped, perfoliate or not.

Flowers usually perfect and staminate (rarely pistillate, perfect and staminate or all perfect). Fruiting pedicels generally erect or recurved to 150°(-180°), rarely decurved. Sepals glabrous or puberulous, distinctly glandular subapically. Paired petals white to lilac or lavender, or yellow to orange, glabrous. Medial petal reduced, generally inconspicuous. Filaments free. Staminodes with bilobed, yellow antherodes. Medial staminode reduced or absent, when present, its antherode commonly different in form from those of the lateral staminodes. Lateral staminodes with straight or arcuate filaments. Lateral stamens with filaments S-shaped, closely parallel or, more commonly, divergent, finely bearded in the distal half on the lower surface, generally with minute, inconspicuous hairs. Medial stamen with anther subequal to the lateral anthers in size but differing in shape (usually with a broader connective) and orientation. Ovary sessile to stipitate, glabrous or puberulous with glandular hairs, dorsal locule usually not developed, occasionally 1-ovulate, ventral locules each 1-3-ovulate, style arcuate-decurved to straight, generally recurved apically, stigma capitate.

Capsules sessile to stipitate, dehiscent, bivalved, bilocular or occasionally trilocular, lustrous, glabrous or puberulous, valves persistent, dorsal locule (when developed) 1-seeded or, by abortion, empty, ventral locules each 1-3-seeded, cells of the capsule wall commonly transversely elongate, occasionally isodiametric or rarely longitudinally elongate. Seeds very variable, in outline circular, elliptic, oblong, ovate or trapezoidal, hilum in a groove or not, testa smooth, rugose, ribbed, sulcate, reticulate, tuberculate or scrobiculate, farinose granules sometimes present, entire testa or parts of it sometimes covered with a thin whitish coating (fused farinose granules?).

BASIC CHROMOSOME NUMBERS.—$x = 10$, 13, and 15.

DISTRIBUTION.—West Africa from N limits of the genus E to S Sudan, SW Ethiopia, W Kenya, and E Tanzania S to Angola, Zambia, Zimbabwe, Swaziland, and South Africa (E Cape Province); *Aneilema umbrosum* also occurs in the neotropics.

Key to the Species of Section *Brevibarbata* Faden

1. Paired petals yellow to orange.
   2. Fruiting pedicels recurved 270°; inflorescences lax or moderately lax; roots fibrous; laminae petiolate . . . . . ***A. angolense***
   2. Fruiting pedicels erect or recurved to ~150°; inflorescences dense; roots tuberous; laminae sessile.
      3. Testa smooth, lacking farinose granules . . . . . ***A. homblei***
      3. Testa furrowed, with farinose granules.
         4. Leaves linear, less than 1 cm wide; flowers 5.5-8.5 mm wide . . . . . ***A. macrorrhizum***
         4. Leaves lanceolate to lanceolate-elliptic, more than 1 cm wide; flowers 9-14 mm wide . . . . . ***A. welwitschii***
1. Paired petals white to lilac or lavender.
   6. Seeds one per ventral locule; capsules as wide as long or wider.
      7. At least the lower laminae petiolate; cincinni always several-flowered; testa foveate-tuberculate or foveate-reticulate, brown.
         8. Sepals glabrous; decumbent perennials . . . . . ***A. dispermum***
         8. Sepals puberulous; annuals.
            9. Pedicels 1.5-3 mm long, erect to slightly further recurved in fruit; cells of the capsule wall transversely elongate . . . . . ***A. arenicola***
            9. Pedicels 2-8 mm long, strongly recurved (120-270°) in fruit; cells of the capsule wall longitudinally elongate or isodiametric.
               10. Cells of the capsule wall longitudinally elongate; inflorescences composed of (6-)10-20(-29) cincinni; seeds dark brown . . . . . ***A. brunneospermum***
               10. Cells of the capsule wall ± isodiametric to slightly longitudinally elongate; inflorescences composed of 3-13 cincinni; seeds pale pinkish gray . . . . . ***A. schlechteri***
      7. All laminae sessile; cincinni 1- or several-flowered; testa ribbed, whitish or pinkish.
         11. Slender annuals; cincinni all 1-flowered; seeds globose.

12. Cincinnus bracts linear, 5–7 mm long . . . . . *A. mortonii*
12. Cincinnus bracts ovate, 1–3 mm long . . . . . *A. paludosum*

11. Tuberous rooted perennials; cincinni several-flowered; seeds longer than wide.
13. Stems slender, internodes mostly exposed near the inflorescence; bristly red hairs absent . . . . . *A. paludosum*
13. Stems more robust, internodes usually not exposed, if more slender and the internodes exposed, then bristly red hairs present on the internodes and sheathes . . . . . *A. setiferum*

6. Seeds 2–3 per ventral locule; capsules longer than wide.
14. Shoots decumbent; roots fibrous; laminae petiolate, lanceolate to ovate; capsules glabrous or puberulous; forest species.
15. Seeds rugose-tuberculate; capsules puberulous; sepals puberulous . . . . . *A. dregeanum*
15. Seeds reticulate-foveate; capsules glabrous or subglabrous; sepals glabrous or sparsely puberulous.
16. Inflorescences moderately lax to moderately dense; fruiting pedicels often decurved; capsules with dorsal locule not developed, with ventral locules each 2-seeded; sepals sometimes sparsely puberulous . . . . . *A. umbrosum*
16. Inflorescences dense; fruiting pedicels erect or further recurved; capsules with dorsal locule frequently developed, 1-seeded or empty, with ventral locules each 2–3-seeded; sepals glabrous.
17. Leaf margins ciliate; capsules acute at apex, very sparsely puberulous . . . . . *A. silvaticum*
17. Leaf margins scabrid, not ciliate; capsules rounded to truncate at apex, glabrous . . . . . *A. beniniense*

14. Shoots erect to ascending, rarely decumbent; roots tuberous; laminae sessile or petiolate, linear to lanceolate; capsules puberulous; savannah species.
18. Plants with basal rosettes of leaves; leaf margins ciliate; flowers opening in the afternoon . . . . . *A. pomeridianum*
18. Plants lacking basal rosettes; leaf margins scabrid but not ciliate; flowers opening in the morning . . . . . *A. lanceolatum*

Species Citations and Distributions

Aneilema angolense C.B. Clarke in Thiselton-Dyer, Fl. Trop. Africa, 8:67, 381, 1901. [Angola.]

Aneilema arenicola Faden, Bothalia, 15:94, 1984. [Mozambique to South Africa (N Natal).]

Aneilema beniniense (P. de Beauvois) Kunth, Enum. Pl., 4:73, 1843. [Basionym: *Commelina beniniensis* P. de Beauvois, Fl. Owar.,2:49, tab. 87, 1816. Senegal to SE Ethiopia S to Angola and Zambia (Plate 4*i*).]

Aneilema brunneospermum Faden, Bothalia, 15:91, 1984. [Mozambique to South Africa (Transvaal and N Natal) and Swaziland (Plate 4*l*).]

Aneilema dispermum Brenan, Kew Bull., 7:198, 1952. [Tanzania to Malawi (plants from Cameroon and Fernando Po may not be conspecific).]

Aneilema dregeanum Kunth, Enum. Pl., 4:73, 1843. [Mozambique to South Africa (Cape and Natal).]

Aneilema homblei De Wildeman, Feddes Repert. Spec. Nov. Regni Veg., 12:290, 1913. [Zaire.]

Aneilema lanceolatum Bentham in Hooker & Bentham, Fl. Nigrit., 546, 1849. [Mali to Sudan S to Congo, Zaire, Uganda and NW Kenya.]

Aneilema macrorrhizum Th. Fries, jr., in R.E. Fries, Schwed. Rhodesia-Kongo Exped., 1:220, fig. 19a–b, p. 221, 1914. [SE Zaire and Zambia to S Tanzania.]

Aneilema mortonii Brenan, Kew Bull., 22:387, 1968. [Ghana.]

Aneilema paludosum A. Chevalier, Mém. Soc. Bot. France, 8:215, 1912. [Senegal to Chad.]

Aneilema pomeridianum Stanfield & Brenan in Brenan, Kew Bull., 15:217, 1961. [Ghana and Nigeria (Plate 4*k*).]

Aneilema schlechteri K. Schumann, Bot. Jahrb. Syst., 33:376, 1903. [SE Zimbabwe to South Africa (Transvaal).]

Aneilema setiferum A. Chevalier, Mém. Soc. Bot. France, 8:215, 1912. [Mali and Guinea Bissau to Nigeria.]

Aneilema silvaticum Brenan, Kew Bull., 7:203, 1952. [Nigeria to N Zaire.]

Aneilema umbrosum (Vahl) Kunth, Enum. Pl., 4:71, 1843. [Basionym: *Commelina umbrosum* Vahl, Enum. Pl., 2:179, 1805–1806. Senegal to S Sudan S to Congo, Zaire and Uganda; also Panama to Venezuela and Grenada S to Bolivia and Brazil.]

Aneilema welwitschii C.B. Clarke in De Candolle, Monogr. Phan., 3:229, 1881. [Angola to S Tanzania and Mozambique (Plate 4*j*).]

Discussion

Section *Brevibarbata* is the largest and most complex section in the genus. It is characterized by small- to medium-sized flowers in which the distal half of the lateral

stamen filaments is minutely and inconspicuously bearded and by the medial anther more or less equal to the lateral anthers in size (but differing in form). The section is mainly centered in western Africa, and it includes several widespread species that are morphologically and cytologically diverse, e.g., *A. beniniense*, *A. umbrosum*, and *A. welwitschii*. Section *Brevibarbata* comprises four species groups: a western African forest group (*A. beniniense*, *A. silvaticum*, *A. umbrousm*, and west African *A. dispermum*, which is probably distinct from the eastern African plant of the same name); a western African savannah group (*A. lanceolatum*, *A. pomeridianum*, *A. setiferum*, *A. paludosum*, and *A. mortonii*); a central African savannah and woodland group with yellow to orange flowers (*A. welwitschii*, *A. homblei*, *A. macrorrhizum*, and *A. angolense*); and an eastern and southern African group of diverse habitats (*A. dispermum*, *A. dregeanum*, *A. schlechteri*, *A. arenicola*, and *A. brunneospermum*). Although many of these taxa have been studied, especially by Morton (1966) and Faden (1984), and a number of infraspecific taxa have been described, we are far from understanding the total variation in this section.

Section 7: *Pedunculosa* Faden, new section

Herbae plerumque annuae radicibus fibrosis, foliis spiraliter dispositis. Inflorescentiae thyrsi densi. Axis inflorescentiae et axes atque pedunculi cincinnorum puberuli trichomatibus unciformibus plerumque biformibus praediti, trichomatibus uniseriatis longisque saepe adjectis. Braeteolae haud perfoliatae apicibus longis, linearibus in glandibus elavatis terminantibus saepe praeditae. Petalum medium deminutum. Filamenta libra. Stamina lateralia filamentis sigmoideis, in dimidio distali dense barbatis. Stamen medium deminutum. Ovarium puberulum trichomatibus glandulosis praeditum sed medidorsaliter glabrum. Capsulae dehiscentes, lucentes, puberulae, loculo dorsali haud evoluto vel 1-seminali, loculis ventralibus uterque 1-3-seminalibus, cellulis parietis capsulae transverse elongatis.

TYPE SPECIES.—*Aneilema pedunculosum* C.B. Clarke.

Annual or less commonly perennial herbs with fibrous roots and spirally arranged leaves.

Inflorescenees dense thyrses, terminal and axillary from the inflorescence braet and upper leaves. Inflorescence braet basal to medial, membranous, enclosing the young inflorescence. Inflorescence axis and cincinnus peduneles and axes puberulous with hook-hairs generally of two sizes, frequently a small number of long, uniseriate hairs also present. Cincinnus axes often abbreviated. Cincinnus braets and bracteoles frequently with long, linear apices terminating in ± elavate glands. Braeteoles never perfoliate.

Flowers perfect and staminate (rarely some pistillate). Fruiting pedicels erect or recurved to ~150°, persistent. Sepals prominently glandular subapically. Paired petals whitish to lilac or bluish purple, glabrous. Medial petal reduced, but sometimes conspicuous. Filaments free. Staminodes with bilobed, yellow antherodes; medial staminode (occasionally absent) similar to the lateral staminodes but filament shorter; lateral staminodes with filaments gently arcuate-decurved. Lateral stamens with filaments S-shaped, densely bearded in the distal half with long, usually brightly colored hairs attached mostly on the lower surface, the part of the filament to which the hairs are attached broadened laterally, anthers small, ovate. Medial stamen shorter than the lateral stamens, with a small, usually dumbbell-shaped anther with small, slightly polleniferous, distal anther sacs. Ovary sessile or subsessile, puberulous with forward-pointing to patent, capitate, glandular hairs predominantly on the ventral and lateral surfaces, glabrous middorsally, dorsal locule usually not developed, occasionally present and containing an ovule, ventral locules each 1-3-ovulate, style arcuate-decurved to straight, sometimes recurved apically, stigma capitate or not enlarged.

Capsules sessile or subsessile, dehiscent, bivalved, bilocular or occasionally trilocular, lustrous, puberulous, apex rounded to truncate or emarginate, valves persistent, rarely the dorsal valve tardily deciduous, dorsal locule (when developed) 1-seeded or, by abortion, empty, ventral locules each 1-3-seeded, cells of the capsule wall transversely elongate. Seeds mostly ovate to trapezoidal or elliptic, apical ventral locule seeds usually rounded apically, basal ventral locule seeds commonly angular basally, hilum in a deep groove or pit, testa rugose or shallowly scrobiculate, sulcate or reticulate-foveate, farinose granules commonly present.

BASIC CHROMOSOME NUMBER.—$x = 9$.

DISTRIBUTION.—SE Sudan and W Ethiopia, S to Namibia (Caprivi Strip), Botswana, Zimbabwe, and Mozambique.

Key to the Species of Section *Pedunculosa* Faden

1. Cincinnus bracts and bracteoles lacking linear, gland-tipped apices; inflorescences lacking long, uniseriate hairs.
   2. Leaves linear to linear-lanceolate, 0.3–1 cm wide; leaf sheaths lacking long hairs at the apex; hilum in a pit . . . . . ***A. richardsiae***
   2. Leaves ovate to lanceolate-elliptic, mostly 1.5–3.2 cm wide; sheaths with long hairs at the apex; hilum in a groove . . . . . ***A. spekei***
1. Cincinnus bracts and bracteoles with linear, gland-tipped apices; inflorescences commonly with long, uniseriate hairs.

3. Leaves with sessile laminae.
   4. Flowers 8–10 mm wide; stamen filaments bearded with maroon hairs; capsules with ventral locules each 1–2-seeded . . . . . ***A. hirtum***
   4. Flowers 13–15 mm wide; stamen filaments bearded with yellow hairs; capsules with ventral locules each 2-seeded . . . . . ***A. chrysopogon***
3. Leaves with petiolate laminae.
   5. Ventral locules usually 1-seeded; solitary cincinnus present at base of peduncle of terminal thyrse, widely separated from other cincinni; petals subequal in width and ± concolorous . . . . . ***A. minutiflorum***
   5. Ventral locules 2–3-seeded (1-seeded only through abortion); no cincinnus present at base of peduncle of terminal thyrse; medial petal narrower than paired petals, differing in color from them.
      6. Seeds 3 per ventral locule, 3-lobed . . . . . ***A. nicholsonii***
      6. Seeds 2 per ventral locule, unlobed or 3-lobed.
         7. Flowers 4–7.5 mm wide; medial staminode lacking; filaments bearded with reddish purple or maroon hairs; seeds 3-lobed . . ***A. termitarium***
         7. Flowers 9–13 mm wide; medial staminode present; filaments bearded with bluish purple hairs; seeds unlobed.
            8. Annuals; dorsal locule well-developed, usually containing a seed . . . . . ***A. pedunculosum***
            8. Decumbent perennials; dorsal locule not developed . . . . ***A. leiocaule***

Species Citations and Distributions

Aneilema chrysopogon Brenan, Kew Bull., 15:222, 1961. [S Tanzania to N Zambia (Plate 4*n*).]

Aneilema hirtum A. Richard, Tent. Fl. Abyssinicae, 3(5):343, 1850. [Ethiopia to Zaire, Zambia, Malawi, and Tanzania (Plate 4*o*).]

Aneilema leiocaule K. Schumann in Engler, Pflanzenwelt Ost-Afrikas C, 136, 1895. [S Ethiopia S to E Zaire and Tanzania (and Zambia?) (Plate 4*m*).]

Aneilema minutiflorum Faden, ined. [(= *Aneilema* sp. *B* of Faden in Agnew, Upland Kenya Wild Fl., 664, 667, 1974].—*Faden & Evans 70/899; Tweedie 759*). W Kenya to Uganda and Tanzania.]

Aneilema nicholsonii C.B. Clarke in Thiselton-Dyer, Fl. Trop. Africa, 8:70, 1901. [S Kenya S to Namibia (Caprivi Strip), Botswana, Zimbabwe, and Mozambique (Plate 4*p*).]

Aneilema pedunculosum C.B. Clarke in De Candolle, Monogr. Phan., 3:228, 1881. [S Tanzania to Zimbabwe and Mozambique.]

Aneilema richardsiae Brenan, Kew Bull., 15:219, 1961. [S Tanzania to E Zaire and N Zambia.]

Aneilema spekei C.B. Clarke in Thiselton-Dyer, Fl. Trop. Africa, 8:71, 1901. [Sudan and Ethiopia S to Zaire, Zambia, and Tanzania.]

Aneilema termitarium Faden, ined. [(*Faden & Faden 74/139*). S Tanzania and E Zaire to Zambia.]

Discussion

Section *Pedunculosa* is very natural. Several unusual characters clearly define it: annual habit (except *A. leiocaule*), dense inflorescences, non-perfoliate bracteoles that often terminate in a clavate, glandular apex, densely bearded (with long, brightly colored hairs) lateral stamen filaments, and reduced medial anther. The basic chromosome number, $x = 9$, is unique to this section and is recorded from all species that have been counted. Although the section is easy to recognize, separating the species is difficult, especially with dried specimens. The main taxonomic problems are the determination of the status of plants that resemble *A. spekei* but have bracteoles with linear apices, e.g., *Renvoize & Abdallah 2251;* the identification of a plant from northern Zambia that resembles *A. leiocaule* (*Richards 1531*); and a study of the variation in *A. hirtum* for which two chromosome numbers are known.

Species of Uncertain Generic Position

In addition to the species included in the seven sections of *Aneilema* recognized above and the species once placed in the genus but here with certainty or high probability excluded from *Aneilema* (see Appendix II), there remain two species that cannot easily be included in the genus but neither can they be readily assigned to other genera. These are described and discussed below.

Aneilema calandrinoides F. Mueller

Aneilema calandrinoides F. Mueller, Frag., 9:191, 1875.

Type.—Australia, Queensland, between the Norman and Gilbert rivers, *T. A. Gulliver s.n.* (MEL, holotype, not seen; BRI, K—2 sheets, isotypes).

Decumbent herbs rooting at the nodes. Roots fibrous, moderately thick (~1–1.5 mm wide). Shoots unbranched (in specimens), up to 14 cm long. Internodes 2–7 cm long, 1–2 mm in diameter, glabrous. Leaves with sheaths 5–14 mm long, glabrous or with some very small, scattered, uniseriate hairs, laminae sessile, apparently slightly fleshy, linear, 1.5–4 cm long (or perhaps longer because none has an apex), 1–3 mm

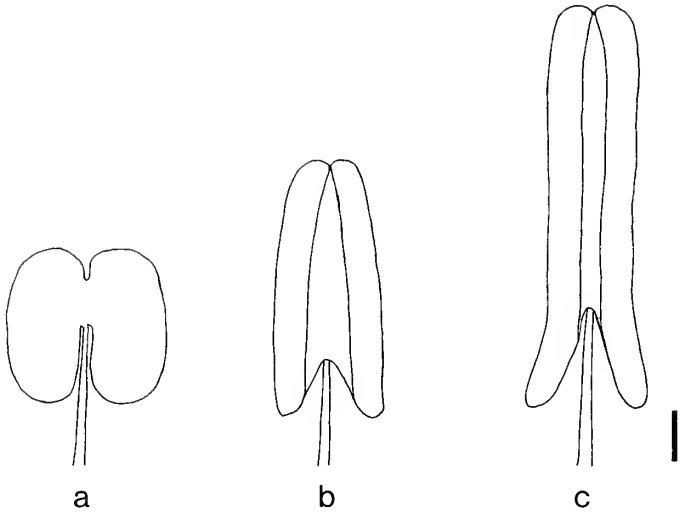


FIGURE 56.—Antherode and anthers of *Aneilema calandrinoides* F. Mueller: *a*, antherode; *b*, lateral anther; *c*, medial anther (from *Gulliver s.n.*—K). (Bar = 0.5 mm.)

wide, base cuneate, margin thickened, glabrous or with a few, minute, uniseriate hairs (and rarely 1 or more hook-hairs?) towards the base, both surfaces glabrous.

Inflorescences consisting of solitary, terminal flowers, which become leaf-opposed. Bracts and bracteoles absent. Flowers apparently ~2.5-3 cm wide. Pedicels erect, 11-22 mm long, glabrous. Sepals sepaloid, subequal, free, one (probably the outer) more strongly hooded than the other two, 8.5-9 mm long, glabrous. Petals free, equal or subequal, 2 cm long, not distinctly clawed, bluish purple. Staminodes 3, all on the side of the flower towards the strongly hooded sepal, subequal, filaments slender, ~5 mm long, glabrous, antherodes bilobed, yellow, lobes sessile, reniform to transversely elliptic, ~0.8 mm long, 1.4-1.6 mm wide (Figure 56*a*). Stamens 3, all on the side of the flower away from the strongly hooded sepal; lateral stamens with filaments ~10 mm long, glabrous, anthers oblong-elliptic, 2-2.8 mm long, connective narrow, anther sacs with basal, free ends divaricate or not (Figure 56*b*); medial stamen with filament ~6 mm long, glabrous, anther oblong, 3-3.8 mm long, connective narrow, anther sacs with basal free ends slightly divaricate (Figure 56*c*). Ovary ~1.5 mm long, 3-angled and probably trilocular, densely covered with papillae or wart-like glands, particularly along the angles, tapering into the style, style S-shaped, ~11 mm long, glabrous, stigma capitate.

Capsules and seeds unknown.

DISTRIBUTION.—Australia (N Queensland).

SPECIMENS SEEN.—AUSTRALIA. QUEENSLAND: Between the Norman and Gilbert rivers, *Gulliver s.n.* (BRI, K—2 sheets); Carpentaria, Carron's Creek, *Gulliver s.n.* (K) [part of the previous collection?].

DISCUSSION

The flowers of this species agree with those of *Aneilema* in stamen and staminode arrangement, form of the staminodes, and differentiation of the medial from the lateral stamens. In some details, e.g., bilobed antherodes and differentiated medial stamen, they are closer to typical *Aneilema* species than are the flowers of *A. neocaledonicum*, a true *Aneilema*. Indeed, the only observable floral difference from *Aneilema* is the papillae or wart-like glands on the ovary. It has not been possible to determine the numbers of locules and ovules because of the limited material.

Although *A. calandrinoides* could readily be accepted as an *Aneilema* on the basis of its floral structure, its inflorescence structure—ebracteate and ebracteolate, one-flowered cincinni—is not only totally unlike that of any species of the genus, but it is also unique in the Commelinaceae. In *Aneilema* the cincinni always have bracts at their bases, and the pedicels are bracteole-opposed. The cincinni are rarely one-flowered, and when they are, they occur in dense thyrses.

Leaf-opposed inflorescences do not occur in *Aneilema*, although, as noted above, each individual flower is bracteole-opposed as in all Commelinaceae that possess bracteoles. On this basis the entire plant of *A. calandrinoides* might be considered equivalent to a single cincinnus of *Aneilema*, with the leaves homologous to the bracteoles and the internodes to the cincinnus axis. Because flowers appear to be borne opposed to every leaf in *A. calandrinoides*, this model has some appeal. The major drawbacks with it are (1) in order to be homologous to a cincinnus, the leaves and flowers in *A. calandrinoides* should be two-ranked, but, unfortunately, none of the shoots is long enough to determine this character, and (2) every internode of *A. calandrinoides* is subtended by a prophyll, which is characteristic of lateral shoots, but prophylls do not occur in cincinni. The cincinnus homology hypothesis therefore is probably incorrect, and it is likely that each flower represents a reduced cincinnus.

I believe that, because of its *Aneilema* floral structure, unique inflorescence, and unusual growth habit, *A. calandrinoides* must be treated either as a very aberrant species of *Aneilema* or as a separate genus. Although I once suggested the latter course (Faden, 1975), I now prefer to await more material before making a final decision. Whatever its generic position, *A. calandrinoides* clearly must have been derived from *Aneilema* section *Aneilema*. The decumbent habit and linear leaves of this species suggest a marsh habitat. None of the Australo-Oceanic *Aneilema* species occurs in such situations. Possibly the adaptation to an aquatic habitat by some ancestral *Aneilema* was accompanied by the radical changes in habit and inflorescence structure that produced *A. calandrinoides*.

Aneilema brasiliense C.B. Clarke

Aneilema brasiliense C.B. Clarke in De Candolle, Monogr. Phan., 3:225, 1881. [Syntypes: Brazil, Piauhy [Piaui] Province, between Cacumbino and Retiro,

Mar 1829, *Gardner 2333* (K (ex Herbarium Hookerianum), lectotype; FHO, K (ex Herbarium Benthamianum), isolectotypes); Bahia, *Blanchet 873* (G—2 sheets, S).]

Erect, unbranched or occasionally sparsely branched, annual herbs to ~50 cm tall. Roots fibrous. Lower internodes elongate (to 10 cm long), uppermost greatly reduced so that the upper leaves are clustered below the inflorescence, all internodes puberulous with hook-hairs or the lower glabrescent. Leaves spirally arranged, sheaths 5–15 mm long, puberulous with hook-hairs, ciliate at the apex; laminae petiolate (except the uppermost), elliptic to lanceolate-elliptic, 6–15 cm long, 2–4.5 cm wide, apex acuminate, base cuneate to broadly cuneate, margins planar, scabrid with prickle-hairs for their entire length, both surfaces sparsely to densely puberulous with hook-hairs, the adaxial scabrid with prickle hairs towards the margin, also occasionally with uniseriate hairs, midrib very prominent on the abaxial surface.

Inflorescence a terminal (and frequently also axillary from the uppermost leaves), lax, obovoid (rarely ovoid) thyrse, 5–13 cm long, 4–12 cm wide, with 1–5 widely spaced, alternate, erect to ascending (rarely patent) cincinni. Peduncles to ~5 cm long, densely puberulous with hook-hairs. Inflorescence axis puberulous with hook-hairs. Cincinni to 9 cm long and 10-flowered. Cincinnus bracts herbaceous or membranous, narrowly lanceolate, 3.5–10(–20) mm long, longest in the lowermost cincinnus, decreasing in size upwards, subglabrous to puberulous with hook-hairs, generally with uniseriate hairs as well, particularly towards their apices, persistent. Cincinnus peduncles exceeding the cincinnus bracts, longest in the lowermost cincinnus, decreasing upwards, (1–)1.5–3.5(–5) cm long, puberulous with hook-hairs. Cincinnus axes puberulous with hook-hairs, also with uniseriate hairs at the nodes. Bracteoles attached (0.8–)3–10(–15) mm apart, herbaceous, lanceolate-ovate to ovate-elliptic, amplexicaul but not perfoliate, 2.5–3.5 mm long, sparsely pilose-puberulous with uniseriate hairs and hook-hairs, glandular(?) near the apex, persistent.

Pedicels 5–7 mm long in flower, to 11 mm long in fruit, ascending in flower, erect in fruit, puberulous with hook-hairs. Sepals sepaloid, free, subequal, 4–7 mm long, sparsely pilose-puberulous with a mixture of hook-hairs and uniseriate hairs, glandular(?) near the apex; medial sepal lanceolate to lanceolate-elliptic, strongly hooded at the apex; lateral sepals narrowly elliptic to oblong, not strongly hooded. Paired petals ~3–5 mm long (or longer?), apparently not to shortly clawed, limb ovate, blue to violet. Medial petal oblong, ~3 mm long × 0.6 mm wide, white(?). Filament bases free. Staminodes absent, or when present, subequal and opposite the outer sepal and paired petals, filaments very slender, glabrous, 1–2 mm long, antherodes unlobed to bilobed with sessile lobes, 0.15–0.5 mm long, 0.2–0.7 mm wide (Figure 57). Lateral stamens opposite the medial petal and lateral sepals, with filaments ± horizontal, straight, then sharply recurved near the apex, 2–6 mm long, glabrous, anthers ovate to ovate-elliptic, 0.7–1.5 mm long, 0.6 mm wide. Medial stamen with filament

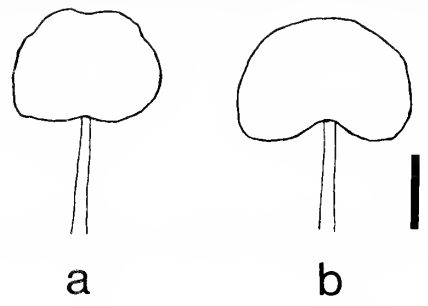


FIGURE 57.—Antherodes of *Aneilema brasiliense* C.B. Clarke: *a*, medial antherode; *b*, lateral antherode (from *Glaziou 12253*—P) (Bar = 0.5 mm.)

arcuate-ascending, ~3 mm long, glabrous, anther broadly elliptic, 0.4–1.3 mm long, 0.45–0.7 mm wide. Ovary sessile, obovate to oblong-elliptic, 1–1.2 mm long, glabrous, apex truncate, dorsal locule humpbacked towards the ovary apex, 1-ovulate, ventral locules 2-ovulate; style 2.5–6 mm long, gently arcuate-decurved for most of its length, then sharply recurved near the apex, stigma very large, capitate.

Capsules sessile, oblong-elliptic to obovate-elliptic, dehiscent, bivalved, trilocular, 5.5–6.5 mm long, 3–3.7 mm wide, tan, dull, glabrous, apex emarginate, valves slightly spreading, persistent, dorsal locule usually (always?) empty, ventral locules 2-seeded, cells of the capsule wall isodiametric, arranged in longitudinal ranks. Seeds ± rectangular, ± truncate at both ends, ~1.7 mm long × 2 mm wide, hilum linear, prominent, raised in a shallow groove, slightly extended onto apical and basal surfaces, embryotega lateral, testa rugose, tan, spotted with dark brown, especially on the bumps, with a very low, fine, irregular, colorless reticulum on the surface.

DISTRIBUTION.—Venezuela and Brazil.

SPECIMENS SEEN.—VENEZUELA. BOLIVAR: San Félix, *Aristeguieta 5807* (K, NY, VEN); La Camilera, 40 km E of El Manteco, *Delascio & Liesner 6989* (US) & *7031* (US); Los Aceites, NE of El Manteco, *Delascio & Liesner 7413* (MO). MONAGAS: Jusepin-Río Amana, *Aristeguieta & Virrueta 7543* (VEN).

BRAZIL. BAHIA: Bahía, *Blanchet 873* (G, S) & *1263* (G). CEARÁ: Ceará, coastal region, *Bollard 5* (K); Serra de Araripe, Novo Eú, *von Lutzelburg 26129* (M). MINAS GERAIS: 15 km W of Januária on road to Serra da Araras, *Anderson 9256*) (F, US). Lagoa Santa, *Warming s.n.* (P). PERNAMBUCO: Tapéra, *Pickel 3062* (US). PIAUI: Between Cacumbino and Retiro, *Gardner 2333* (FHO, K). RIO DE JANEIRO: Environs de Rio [de] Janeiro, Larangeiras, chez les Princes, *Glaziou 12253* (B, K, P).

DISCUSSION

The most outstanding characters of *A. brasiliense* are its annual habit, very lax inflorescences with few cincinni, non-perfoliate bracteoles, sepals covered with a mixture of hook-hairs and uniseriate hairs, oblong medial petal, lack of

staminodes or, when present, their antherodes sometimes not bilobed, horizontal lateral stamens, glabrous ovary and capsule, and isodiametric cells of the capsule wall. The combination of these characters and the exclusive South American distribution of *A. brasiliense* readily separates it from all other species of *Aneilema*. The question remains as to whether *A. brasiliense* is sufficiently similar to other *Aneilema* species to merit retention in the genus.

Aneilema brasiliense occupies the same position relative to the rest of *Aneilema* as does the genus *Rhopalephora:* it has very few characters that are otherwise unknown in *Aneilema,* e.g., oblong medial petal and complete lack of staminodes, but it combines a number of unusual ones so that associating *A. brasiliense* with any section of *Aneilema* is difficult.

Overall, *Aneilema brasiliense* appears to be closest to species in section *Aneilema* or section *Amelina*. From the former it differs in its annual habit, bracteole form and pubescence, sepal pubescence type, reduced medial petal, shape of the cells of the capsule wall, and much longer hilum. *Aneilema brasiliense* differs from section *Amelina,* itself a rather heterogeneous group of species, in habit (only *A. ephemerum* of section *Amelina* is annual), cincinnus arrangement (*A. longirrhizum* has mostly alternate cincinni), bracteole form and pubescence (bracteoles not perfoliate in *A. gillettii*), medial petal and antherode form, and glabrous ovary and capsule (capsule glabrous in *A. johnstonii,* nearly glabrous in *A. gillettii*).

Besides *A. brasiliense,* the only neotropical *Aneilema* is *A. umbrosum* subsp. *ovato-oblongum,* a West African taxon that presumably has been introduced into the neotropics (Faden, 1978c). It belongs to section *Brevibarbata* and is clearly unrelated to *A. brasiliense.*

I believe that there are only two reasonable alternatives for the taxonomic treatment of *A. brasiliense*: (1) inclusion in *Aneilema* as a distinct section, or (2) exclusion and treatment as a separate, monotypic genus as was suggested by Clarke (1881a,b). A final decision must await more conclusive evidence obtainable only from living material.

Appendix I

Rejected Generic Synonyms of *Aneilema*

The genus *Aneilema* has been used in a much broader sense in the past than it is here. As a result, a number of generic names, formerly treated as synonyms of it, are now considered valid genera themselves or synonyms of other genera. These rejected generic synonyms of *Aneilema,* along with their present status, are as follows:

Aphylax Salisbury, Trans. Hort. Soc. London, 1:271, 1812 [nom. nud. = *Murdannia* Royle].

Dichaespermum Wight ["Dichoespermum"], Icon. Pl. Ind. Orient., 6:31, 1853 [= *Murdannia*].

Dictyospermum Wight, Icon. Pl. Ind. Orient., 6:29, 1853 [= distinct genus].

Dilasia Rafinesque, Fl. Tellur., 4:122, 1838 [= *Murdannia*].

Ditelesia Rafinesque, Fl. Tellur., 3:69, 1837 [= *Murdannia*].

Murdannia Royle, Illus. Bot. Himalayan Mts., 403, tab. 95, fig. 3, 1840 [nom. cons. = distinct genus].

Piletocarpus Hasskarl, Flora, 49:212, 1866 [in clavi]; Commel. Ind., 14, 1870 [= *Rhopalephora* Hasskarl].

Prionostachys Hasskarl, Flora, 49:212, 1866 [in clavi] [= *Murdannia*].

Rhopalephora Hasskarl, Bot. Zeitung (Berlin), 1864:58, 1864 [= distinct genus].

Streptylis Rafinesque, Fl. Tellur., 4:122, 1838 [= *Murdannia*].

Talipula Rafinesque, Fl. Tellur., 2:17, 1837 [= *Murdannia*].

Appendix II

Index to Specific Epithets in *Aneilema*

Epithets referable to a variety of genera have been included in *Aneilema* at one time or another. Their present status, when known, is given below. Correct names for species in *Aneilema* are in roman type. Specific names used in the text above but not yet published are listed as "Faden, nom. nud."

acuminatum R. Brown
acutifolium Lauterbach & K. Schumann = *Murdannia acutifolia* (Lauterbach & K. Schumann) Faden, new combination (Basionym: *Aneilema acutifolia* Lauterbach & K. Schumann in Schumann and Lauterbach, Fl. deutsch. Schutzgebiete Südsee, 217, 1900)
adhaerans Kunth = A. aequinoctiale
aequinoctiale (P. de Beauvois) G. Don
affine R. Brown = *Murdannia graminea* (R. Brown) Brückner
affine De Wildeman, nom. illeg. (non *A. affine* R. Brown) = A. silvaticum
africanum P. de Beauvois = *Floscopa africana* (P. de Beauvois) C.B. Clarke
aguense (Standley & Steyermark) Standley & Steyermark = *Gibasis triflora* (Martens & Galeotti) D.R. Hunt?
allardii De Wildeman = *Murdannia allardii* (De Wildeman) Brenan
ambiguum (P. de Beauvois) G. Don = *Palisota ambigua* (P. de Beauvois) C.B. Clarke
angolense C.B. Clarke
angustifolium N.E. Brown = *Murdannia*
angustifolium De Wildeman, nom. illeg. (non *A. angustifolium* N.E. Brown) = A. macrorrhizum
anthericoides R. Brown = *Murdannia graminea* (R. Brown) Brückner
aparine Perrier de la Bâthie
arenicola Faden
asperum Buchanan-Hamilton ex Wallich, nom. nud. = *Floscopa scandens* Loureiro
azureum Merrill = *Murdannia spectabilis* (Kurz) Faden

benadirense Chiovenda
beniniense (P. de Beauvois) Kunth
biflorum R. Brown
blumei (Hasskarl) Bakhuizen van den Brink f. = *Murdannia blumei* (Hasskarl) Brenan
bodinieri Léveillé & Vaniot = *Murdannia hookeri* (C.B. Clarke) Brückner
bracteatum (C.B. Clarke) Kuntze = *Murdannia bracteata* (C.B. Clarke) J.K. Morton ex Hong
bracteolatum Martius = A. umbrosum
brasiliense C.B. Clarke, generic status uncertain (see p. 150)
brenanianum Faden
brunneospermum Faden
buaricum Mildbraed ex J.K. Morton, nom. nud. pro syn. = A. lanceolatum

calandrinoides F. Mueller, generic status uncertain (see p. 148)
calceolus Brenan
canaliculatum Dalzell = *Murdannia spirata* (L.) Brückner
cavaleriei Léveillé & Vaniot = *Murdannia simplex* (Vahl) Brenan, new synonymy
chihuahuense (Standley) Woodson = *Gibasis chihuahuensis* (Standley) Rohweder
chrysanthum K. Schumann = A. petersii
chrysopogon Brenan
clandestinum Ridley = *Murdannia clandestina* (Ridley) Faden, new combination (Basionym: *Aneilema clandestinum* Ridley in J. Roy. Asian Soc.Straits, 57:108, 1911)
clarkei Rendle
collinum (Brandegee) Matuda = *Gibasis karwinskyana* (J.A. & J.H. Schultes) Rohweder
compressum Dalzell = *Murdannia nudiflora* (L.) Brenan
conspicuum (Blume) Kunth = *Dictyospermum conspicuum* (Blume) Hasskarl
cordatum Buchanan-Hamilton ex Wallich, nom. nud. = *Murdannia*
coreanum Léveillé & Vaniot = *Murdannia keisak* (Hasskarl) Handel-Mazzetti
crispatum R. Brown = *Pollia crispata* (R. Brown) Bentham
croceum Griffith = *Murdannia crocea* (Griffith) Faden
cymosum (Blume) Kunth = *Floscopa scandens* Loureiro

debile Wallich, nom. nud. = *Murdannia nudiflora* (L.) Brenan
delicatulum C.B. Clarke ex Jex-Blake, nom. subnud. = *Murdannia clarkeana* Brenan
densiflorum (Blume) Kunth = *Floscopa scandens* Loureiro
densum Th. Fries, jr. = A. welwitschii
diandrum Buchanan-Hamilton ex Wallich, nom. nud. = *Murdannia nudiflora* (L.) Brenan

didymum Buchanan-Hamilton ex Wallich, nom. nud. = *Pollia*
didymum Seemann, nom. nud. = *Pollia*
dimorphum Dalzell = *Murdannia dimorpha* (Dalzell) Brückner
discretum Craib = *Murdannia*
dispermum Brenan
divergens C.B. Clarke = *Murdannia divergens* (C.B. Clarke) Brückner
diversifolium Hasskarl = *Murdannia nudiflora* (L.) Brenan
dregeanum Kunth

ecuadoriense Steyermark = *Dichorisandra*
ehrenbergii (Hasskarl) C.B. Clarke = A. forskalii
elatum (Vahl) Kunth = *Murdannia japonica* (Thunberg) Faden
elatum (Vahl) Dalzell = *Murdannia japonica* (Thunberg) Faden
ensifolium Wight = *Murdannia gigantea* (Vahl) Brückner
ephemerum Faden, nom. nud.
erectum De Wildeman = A. welwitschii
esculentum Wallich ex C.B. Clarke = *Murdannia esculenta* (Wallich ex C.B.Clarke) Raizada ex Rolla Rao & Kammathy

fasciatum Warburg ex Lauterbach = *Murdannia*
filiforme Buchanan-Hamilton ex Wallich, nom. nud. = *Murdannia vaginata* (L.) Brückner
filipes Martius = *Gibasis geniculata* (Jacquin) Rohweder
florentii De Wildeman = A. welwitschii
floribundum (Kunth) Hooker & Arnott = *Tripogandra multiflora* (Swartz) Rafinesque
foliosum Hasskarl = *Murdannia nudiflora* (L.) Brenan?
formosanum N.E. Brown = *Murdannia edulis* (Stokes) Faden
forskalii Kunth

gardneri Seubert = *Murdannia gardneri* (Seubert) Brückner
geniculatum (Jacquin) Woodson = *Gibasis geniculata* (Jacquin) Rohweder
giganteum (Vahl) R. Brown = *Murdannia gigantea* (Vahl) Brückner
gillettii Brenan
glanduliferum Joseph & Rolla Rao = *Tricarpelema glanduliferum* (Joseph & Rolla Rao) Faden, new combination (Basionym: *Aneilema glanduliferum* Joseph & Rolla Rao, J. Ind. Bot. Soc., 47:367, 1968)
glaucum Thwaites ex C.B. Clarke = *Murdannia glauca* (Thwaites ex C.B. Clarke) Brückner
gracile (Kotschy & Peyritsch) C.B. Clarke = A. lanceolatum
gracile (Kunth) Steyermark, nom. illeg. (non *A. gracile* (Kotschy & Peyritsch) C.B. Clarke) = *Callisia gracilis* (Kunth) D.R. Hunt
gramineum R. Brown = *Murdannia graminea* (R. Brown) Brückner
grandibracteolatum Faden
greenmanii Woodson = *Thyrsanthemum macrophyllum* (Greenman) Rohweder

hallbergii Blatter = *Dictyospermum ovalifolium* Wight
hamiltonianum Wallich ex C.B. Clarke = *Murdannia blumei* (Hasskarl) Brenan
herbaceum (Roxburgh) Wallich = *Murdannia japonica* (Thunberg) Faden
heterophyllum (Brandegee) Matuda = *Gibasis venustula* (Kunth) D.R. Hunt subsp. *peninsulae* D.R. Hunt
hirticeps C.B. Clarke ex J.K. Morton, nom. nud. pro syn. = A. welwitschii
hirtum A. Richard
hispidum D. Don = *Floscopa scandens* Loureiro
hockii De Wildeman
holosericeum (Kunth) Woodson = *Thyrsanthemum floribundum* (Martens & Galeotti) Pichon
homblei De Wildeman
hookeri C.B. Clarke = *Murdannia hookeri* (C.B. Clarke) Brückner
humile Warburg = *Dictyospermum humile* (Warburg) J.K. Morton
humile Merrill, nom. illeg. (non *A. humile* Warburg) = *Tricarpelema philippense* (Panigrahi) Faden, new combination (Basionym: *Dictyospermum philippense* Panigrahi, Phytologia, 29:338, 1975)

imberbe Ridley = *Dictyospermum conspicuum* (Blume) Hasskarl
imbricatum Warburg = *Pollia*
indehiscens Faden
irregularibracteatum Kew Bulletin, sphalm. = *Senecio irregularibracteatum* De Wildeman

japonicum (Thunberg) Kunth = *Murdannia japonica* (Thunberg) Faden
japonicum Maximowicz = *Pollia secundiflora* (Blume) Bakhuizen van den Brink f.?
johnstonii K. Schumann
junghuhnianum Miquel = *Murdannia nudiflora* (L.) Brenan

kainanense Masamune = *Murdannia kainanensis* (Masamune) Hong
karwinskyanum (J.A. & J.H. Schultes) Woodson = *Gibasis karwinskyana* (J.A. & J.H. Schultes) Rohweder
katangense De Wildeman = A. welwitschii
keisak Hasskarl = *Murdannia keisak* (Hasskarl) Handel-Mazzetti
keyense Warburg = *Rhopalephora vitiensis* (Seemann) Faden
koenigii Wallich ex C.B. Clarke = *Murdannia lanceolata* (Wight) Kammathy
kuntzei C.B. Clarke ex Kuntze, nom. nud. pro syn. = *Murdannia bracteata* (C.B. Clarke) J.K. Morton ex Hong

lamuense Faden
lanceolatum Bentham
lancifolium Griffith = *Murdannia nudiflora* (L.) Brenan

lanufolium Griffith, sphalm. = praec.
lanuginosum Wallich ex C.B. Clarke = *Murdannia lanuginosa* (Wallich ex C. B. Clarke) Brückner
latifolium Wight = *Murdannia japonica* (Thunberg) Faden
laxiflorum Bentham ex C.B. Clarke, nom. nud. pro syn. = A. umbrosum
laxum R. Brown = A. acuminatum
leiocaule K. Schumann
leptospermum K. Schumann ex Faden, nom. nud. pro syn. = A. petersii
lineare (Bentham) Woodson = *Gibasis linearis* (Bentham) Rohweder
lineolatum (Blume) Kunth = *Murdannia japonica* (Thunberg) Faden
longicapsa Faden
longifolium Hooker = *Murdannia simplex* (Vahl) Brenan
longifolium Wallich, nom. nud. = *Murdannia*
longirrhizum Faden
loriforme Hasskarl = *Murdannia loriformis* (Hasskarl) Rolla Rao & Kammathy
loureirii Hance = *Murdannia edulis* (Stokes) Faden
loureiroi Index Kewensis = praec.
lujai De Wildeman & Th. Durand = A. lanceolatum

macrophyllum R. Brown = *Pollia macrophylla* (R. Brown) Bentham
macrorrhizum Th. Fries, jr.
malabaricum (L.) Merrill = *Murdannia nudiflora* (L.) Brenan
medicum (Loureiro) Kostelesky = *Murdannia medica* (Loureiro) Hong
melanostictum Hance = *Murdannia spirata* (L.) Brückner
micranthum (Vahl) Kunth = *Rhopalephora micrantha* (Vahl) Faden
minutiflorum Faden, nom. nud.
minutum (Blume) Kunth = *Murdannia nudiflora* (L.) Brenan?
monadelphum (Blume) Kunth = *Rhopalephora micrantha* (Vahl) Faden
montanum (Wight) Wallich ex C.B. Clarke = *Dictyospermum montanum* Wight
mortehanii De Wildeman = A. beniniense
mortonii Brenan
multiscaposum Lauterbach = *Murdannia edulis* (Stokes) Faden

nanum (Roxburgh) Kunth = *Murdannia spirata* (L.) Brückner
neocaledonicum Schlechter
nicholsonii C.B. Clarke
nigritianum (C.B. Clarke) Hutchinson ex Hutchinson & Dalziel = A. umbrosum subsp. umbrosum
nudicaule (N.L. Burmann) G. Don = *Murdannia nudiflora* (L.) Brenan
nudiflorum (L.) Sweet = *Murdannia nudiflora* (L.) Brenan
nummularium Miquel = *Murdannia spirata* (L.) Brückner
nutans Léveillé = *Murdannia triquetra* (Wallich ex C.B. Clarke) Brückner
nyasense C.B. Clarke

obbiadense Chiovenda
ochraceum Dalzell = *Murdannia crocea* (Griffith) Faden subsp. *ochracea* (Dalzell) Faden
octospermum C.B. Clarke ex Brenan, nom. nud. pro syn. = A. rendlei
oliganthum Franchet & Savatier = *Murdannia keisak* (Hasskarl) Handel-Mazzetti
ovalifolium (Wight) Hooker f. ex C.B. Clarke = *Dictyospermum ovalifolium* Wight
ovato-oblongum P. de Beauvois = A. umbrosum subsp. ovato-oblongum (P. de Beauvois) J.K. Morton
ovatum (Hasskarl) Wallich ex C.B. Clarke = *Dictyospermum ovatum* Hasskarl

paludosum A. Chevalier
paniculatum Wight = *Murdannia dimorpha* (Dalzell) Brückner
paniculatum Wight ex C.B. Clarke, nom. illeg. (non *A. paniculatum* Wight) = *Murdannia semiteres* (Dalzell) Santapau
papuanum Warburg = A. acuminatum
paraguayense C.B. Clarke ex Chodat = *Murdannia paraguayensis* (C.B. Clarke ex Chodat) Brückner
pauciflorum Dalzell = *Murdannia vaginata* (L.) Brückner
pauciflorum Wight, nom. illeg. (non *A. pauciflorum* Dalzell) = *Murdannia pauciflora* Brückner
pauciflorum (Urban & Ekman) Alain, nom. illeg. (non *A. pauciflorum* Dalzell) = *Gibasis*
paucifolium N.E. Brown = *Murdannia medica* (Loureiro) Hong
pedunculosum C.B. Clarke
petersii (Hasskarl) C.B. Clarke
pilosum Wallich, nom. nud. = *Murdannia crocea* (Griffith) Faden
pinetorum (Greene) Matuda = *Tradescantia pinetorum* Greene
plagiocapsa K. Schumann
platyphyllum Merrill = *Murdannia edulis* (Stokes) Faden
poaeoides Seubert = *Callisia filiformis* (Martens & Galeotti) D.R. Hunt
pomeridianum Stanfield & Brenan
protensum (Wight) Wallich ex C.B. Clarke = *Rhopalephora scaberrima* (Blume) Faden
puberulum Hasskarl, sphalm. = A. lanceolatum
pulchellum (Kunth) Woodson = *Gibasis pulchella* (Kunth) Rafinesque
pulneyense Fyson = *Murdannia esculenta* (Wallich ex C.B. Clarke) Raizada ex Rao Rolla & Kammathy?
pusillum Chiovenda

radicans D. Don = *Murdannia nudiflora* (L.) Brenan
recurvatum Faden
rendlei C.B. Clarke
reniforme Buchanan-Hamilton ex Wallich, nom. nud. = *Pollia*
rhodospermum K. Schumann ex C.B. Clarke, nom. nud. pro syn. = A. silvaticum
richardsiae Brenan
rigidum Blatter = *Murdannia simplex* (Vahl) Brenan

ringoetii De Wildeman = *A. hirtum*
rivulare A. Richard = *Floscopa glomerata* (Willdenow ex J.A. & J.H. Schultes) Hasskarl
rugosum Perrier de la Bâthie = *Rhopalephora rugosa* (Perrier de la Bâthie) Faden
russeggeri (Fenzl) C.B. Clarke ("russegeri" sphalm.) = A. lanceolatum

sacleuxii Hua = A. petersii
scaberrimum (Blume) Kunth = *Rhopalephora scaberrima* (Blume) Faden
scapiflorum (Roxburgh) Kostelesky = *Murdannia edulis* (Stokes) Faden
schlechteri K. Schumann
schomburgkianum Kunth = *Murdannia schomburgkiana* (Kunth) Brückner
schweinfurthii Baker ex C.B. Clarke = A. lanceolatum
sclerocarpum F. Mueller
sebitense Faden
secundiflorum (Blume) Kunth = *Pollia secundiflora* (Blume) Bakhuizen van den Brink f.
secundum Wight = *Murdannia simplex* (Vahl) Brenan
semifoliatum C.B. Clarke = *Murdannia semifoliata* (C.B. Clarke) Brückner
semiteres Dalzell = *Murdannia semiteres* (Dalzell) Santapau
sepalosum C.B. Clarke = *Anthericopsis sepalosa* (C.B. Clarke) Engler
serotinum D. Don ex C.B. Clarke, nom. nud. pro syn. = *Murdannia edulis* (Stokes) Faden
serrulatum (Vahl) G. Don = *Tripogandra serrulata* (Vahl) Handlos
sessilifolium (Bentham) J.K. Morton, pro syn. = A. beniniense subsp. sessifolium (Bentham) J.K. Morton
setiferum A. Chevalier
siamense Craib = *Pollia secundiflora* (Blume) Bakhuizen van den Brink f.
sienneum Blatter = *Murdannia lanuginosa* (Wallich ex C.B. Clarke) Brückner
siliculosum R. Brown
silvaticum Brenan
simplex (Vahl) Kunth = *Murdannia simplex* (Vahl) Brenan
sinicum Ker-Gawler = praec.
smithii C.B. Clarke = A. somaliense
somaliense C.B. Clarke
soudanicum C.B. Clarke = A. lanceolatum
spectabile Kurz = *Murdannia spectabilis* (Kurz) Faden
spekei C.B. Clarke
spicatum Wallich, nom. nud. = *Murdannia spectabilis* (Kurz) Faden
spiratum (L.) Sweet = *Murdannia spirata* (L.) Brückner
stenothyrsum Diels = *Murdannia stenothyrsa* (Diels) Handel-Mazzetti
stolzii Mildbraed ex J.K. Morton, nom. nud. pro syn. = A. hirtum
subnudum A. Chevalier = A. lanceolatum subsp. subnudum (A. Chevalier) J.K. Morton
subovatum Ridley = *Dictyospermum ovatum* Hasskarl
succulentum Faden

tacazzeanum Hochstetter ex A. Richard = A. forskalii
tacazzeanum Hochstetter ex C.B. Clarke = A. forskalii
tanaense Faden
taquetii Léveillé = *Murdannia keisak* (Hasskarl) Handel-Mazzetti
taylorii C.B. Clarke
tenerum Baker = *Pseudoparis tenera* (Baker) Faden, new combination (Basionym: *Aneilema tenerum* Baker in J. Linn. Soc., Bot., 22:530, 1887)
tenuissimum (A. Chevalier) A. Chevalier ex Hutchinson & Dalziel = *Murdannia tenuissima* (A. Chevalier) Brenan
terminale Wight = *Murdannia loriformis* (Hasskarl) Rolla Rao & Kammathy
terminale (Blume) Boldingh ex Haines, nom. illeg. (non *A. terminale* Wight), probably = *Cyanotis moluccana* (Roxburgh) Merrill
termitarium Faden, nom. nud.
tetraspermum K. Schumann = A. petersii
thomsonii (C.B. Clarke) C.B. Clarke = *Tricarpelema giganteum* (Hasskarl) Hara
trichocoleum Schauer = *Murdannia nudiflora* (L.) Brenan
triquetrum Wallich ex C.B. Clarke = *Murdannia triquetra* (Wallich ex C.B. Clarke) Brückner
tuberosum Buchanan-Hamilton ex Wallich, nom. nud. = *Murdannia edulis* (Stokes) Faden

umbrosum (Vahl) Kunth
urbinanum (Greenman) Matuda = *Gibasis*
usambarense Faden

vaginatum (L.) Wallich = *Murdannia vaginata* (L.) Brückner
vankerckhovenii De Wildeman = A. nyasense
versicolor Dalzell = *Murdannia versicolor* (Dalzell) Brückner
violaceum F. Mueller ex C.B. Clarke, nom. nud. pro syn. = *Murdannia graminea* (R. Brown) Brückner
vitiense Seemann = *Rhopalephora vitiensis* (Seemann) Faden

welwitschii C.B. Clarke
whytei C.B. Clarke = A. hirtum
wildii Merxmüller = A. hockii
woodii Faden

zebrinum Chiovenda
zeylanicum C.B. Clarke = *Murdannia zeylanica* (C.B. Clarke) Brückner

Appendix III

Specimens Cited

All collections of *Aneilema* taxa belonging to sections *Rendlei, Somaliensia,* and *Lamprodithyros,* but none belonging to other sections, are listed. The first number in parentheses refers to the section, the second to the species within the section. A letter following the species number refers to a subspecies or hybrid (when applicable). A full list of the taxa and their corresponding numbers is given in the table of contents.

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Archbold 713 (3-3); 1408 (3-1); 1491 (5-1a); 1897 (3-3).
Ash 823 (4-1).
Aylmer 182 (5-5).

Baldrati 933 (5-5); 1387 (5-5); 1388 (5-5).
Bally B8534 (3-3); B10133 (4-1); B12145 (5-13); B12193 (5-13); B12348 (5-13); B12692 (3-3); B13592 (3-3); B13931 (5-13).
Bally & Smith B14320 (5-13); B14357 (5-1a).
Barbosa 655 (5-2b).
Barbosa & Lemos 8431 (5-2b).
Batty 162 (5-1a).
Bax 368 (5-1b).
Bayliss BS7216 (5-2b).
Beckett 1022 (4-5c).
Birnie 9 (5-2c).
Boaler 626 (5-1a).
Boivin s.n. (5-1a).
Borle 364 (5-2b).
Botany Students in DSM1351 (5-9).
Botta s.n. (5-5).
Braun 1377 (5-1a); 3624 (5-1a).
Bredenkamp 1795 (5-2b).
Brenan 14232 (5-2b); 14243 (5-13).
Buchanan s.n. (3-3).
Busse 2281 (5-1a); 3054 (5-1a).

Carter & Stannard 652 (4-1); 692 (4-1).
Carvalho s.n. (5-1a).
Ciferri 73 (5-7).
Codd 6891 (5-2b).
Compton 28610 (5-2b).
Corradi 2154 (5-13); 2155 (5-13); 2159 (3-3); 2160 (3-3); 2163 (5-13); 2196 (4-1).
Cufodontis 319 (4-1); 705 (5-1a).

Davey D79 (4-1).
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Faden 69/1300 (5-3); 69/1300A (5-2c); 69/1608 (5-3); 69/1642 (5-3); 69/1699 (5-3); 69/1802 (5-3); 69/1933 (5-3).
Faden & Beentje 85/69 (5-10).
Faden & Evans 70/782 (5-12); 70/788 (3-3); 70/819 (5-1a); 71/498 (3-4); 71/513 (3-4); 71/620 (5-12); 71/714 (5-10); 71/726 (5-10).
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Faulkner 838 (5–1a); 1160 (5–2a); 3670 (5–1a); 4045 (5–9); 4471 (5–2a); s.n. (5–1a).
Faulkner in K712 (5–1a).
Fiori 874 (5–5); 875 (5–5).
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Gillett & Mathew 19068 (5–1b); 19073 (5–1b); 19090 (5–1b).
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Gomes & Sousa 3441 (5–2b); s.n. (5–2b).
Graham 1848 (5–1a); 1903 (5–1a); 3019 (5–3).
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Greenway & Kanuri 11871 (5–1b).
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Harris & Procter 1018 (5–9).
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Index

This index includes all scientific names of Commelinaceae that are mentioned in the text and appendices. Synonyms and page number of the principal reference for a taxon that is described in the text are in italics. Numbers in brackets refer to page numbers of figures and maps.

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